



NATIONAL COUNCIL FOR AIR AND STREAM IMPROVEMENT

**RIPARIAN ZONE FOREST MANAGEMENT
AND THE PROTECTION OF BIODIVERSITY:
A PROBLEM ANALYSIS**

TECHNICAL BULLETIN NO. 908

OCTOBER 2005

by

Daniel A. Sarr, Ph.D.

National Park Service (Ashland, Oregon)

Dennis C. Odion, Ph.D.

Institute for Computational Earth Systems Science, University of California (Santa Barbara, California)

David E. Hibbs, Ph.D.

Department of Forest Science, Oregon State University (Corvallis, Oregon)

Jennifer Weikel (Corvallis, Oregon)

Robert E. Gresswell, Ph.D. and R. Bruce Bury, Ph.D.

US Geological Survey (Corvallis, Oregon)

Nicole M. Czarnomski, Robert J. Pabst, Jeff Shatford and Andrew R. Moldenke, Ph.D.

Oregon State University (Corvallis, Oregon)

Acknowledgments

The authors would like to thank NCASI and Dr. Larry L. Irwin for supporting this project. Helpful feedback was provided by Ed Arnett, Bob Beschta, John Hayes and Bruce McCune.

For more information about this research, contact:

Larry Irwin, Ph.D.
Principal Research Scientist
NCASI
P.O. Box 68
Stevensville, MT 59870
(406) 777-7215
llirwin@bitterroot.net

Alan A. Lucier, Ph.D.
Senior Vice President
NCASI
P.O. Box 13318
Research Triangle Park, NC 27709-3318
(919) 941-6403
alucier@ncasi.org

For information about NCASI publications, contact:

Publications Coordinator
NCASI
P.O. Box 13318
Research Triangle Park, NC 27709-3318
(919) 941-6400
publications@ncasi.org

National Council for Air and Stream Improvement, Inc. (NCASI). 2005. *Riparian zone forest management and the protection of biodiversity: A problem analysis*. Technical Bulletin No. 908. Research Triangle Park, N.C.: National Council for Air and Stream Improvement, Inc.



servicing the environmental research needs of the forest products industry since 1943

PRESIDENT'S NOTE

Forestry practices have complex effects on the biological diversity of forest ecosystems. Forest management activities in riparian (streamside) zones are thought to have especially important effects. Riparian forests provide habitat for many aquatic and terrestrial species and have important ecological functions such as regulating stream temperatures and supplying organic matter to stream channels. It is not surprising that forestry BMPs and regulations often place special emphasis on riparian zone management.

Riparian forest management and its effects on biological diversity are important and controversial topics in the Pacific Northwest. Federal and state regulations affecting riparian zone management are major factors affecting wood supplies and economic returns to public and private forest owners in the region.

NCASI has been an active participant in research on riparian forest management since the late 1970s in partnership with agencies, universities, and member companies. Excellent progress has been made in documenting the ecological functions of riparian zones and in developing riparian BMPs that greatly reduce the impacts of forestry operations on water quality. Today, the scientific and policy debate about riparian forest management in the Pacific Northwest is focused on the degree to which BMPs and alternative prescriptions are effective in conserving important aspects of biological diversity including species that are imperiled and/or highly sensitive to disturbance.

This report provides an overview of the latest scientific information and expert opinion on riparian forest management and its effects on biological diversity in the Pacific Northwest. NCASI contracted with Dr. Daniel Sarr of the National Park Service to organize a multidisciplinary writing team and provide overall leadership for the project. Dr. Larry Irwin, Manager of NCASI's Western Wildlife Program, worked with Dr. Sarr on designing the project and editing this report.

In Part 1, the report's lead authors discuss what is meant by the often misused concept of biodiversity, and describe how natural processes of disturbance create the habitat heterogeneity that, at a range of scales, provides for biodiversity. Although forestry disturbances and natural disturbances can be distinguished, the authors describe how both can be evaluated in terms of their effects on biodiversity by assessing how they influence habitat heterogeneity, as well as legacy retention, physiological stress, and resource availability. These can all be assessed together in the graphical model developed by the authors.

In Part 2, the report addresses forest management effects on specific elements of biodiversity in sections prepared by experts on several taxonomic groups of aquatic and terrestrial organisms. In Part 3, the lead authors provide a synthesis of the taxa-specific information and propose some general principles and approaches to the protection of riparian biodiversity that may be employed at stand or landscape scales. The authors note that aligning forestry treatments to attempt to emulate natural disturbance regimes in landscapes has received much recent attention as the best approach in this regard. However, doing so may not be cost-effective or feasible in some landscapes. The review also

points out that there are both merits and limitations to the riparian buffer approach to protecting biodiversity. The authors identify major gaps in ecological information on these topics, and the report concludes with a research agenda and a framework for critically evaluating past research.

The information, interpretation, and recommendations presented by the authors of this report have important implications for NCASI priorities. For example, it seems clear that perceptions of forestry impacts on biodiversity are influenced to a considerable extent by historical practices (e.g., harvesting without BMPs) and stand-level studies that may have limited relevance to current practices and landscape-level effects.

A handwritten signature in black ink, appearing to read "Ron Yeske". The signature is fluid and cursive, with a long horizontal stroke at the end.

Ronald A. Yeske

October 2005

MOT DU PRÉSIDENT

Les pratiques forestières produisent des effets complexes sur la diversité biologique des écosystèmes forestiers. On estime que les activités d'aménagement forestier dans les bandes riveraines produisent des effets particulièrement importants. Les forêts riveraines fournissent un habitat pour plusieurs espèces aquatiques et terrestres. Elles possèdent d'importantes fonctions écologiques telles que le contrôle de la température des cours d'eau ainsi que l'acheminement de la matière organique dans les lits des cours d'eau. Il va de soi que l'on retrouve dans les meilleures pratiques d'aménagement forestier (MPAF) et la réglementation, une attention particulière à l'aménagement de la bande riveraine.

Sur la côte nord ouest du Pacifique, l'aménagement de la forêt riveraine et ses effets sur la diversité biologique constituent un domaine d'activité de premier plan, quoique controversé. Les réglementations fédérale et étatiques s'appliquant à l'aménagement de la bande riveraine sont des facteurs majeurs affectant l'approvisionnement en fibres et les bénéfices économiques pour le public et les propriétaires de forêts privées dans la région.

NCASI a activement participé aux recherches portant sur l'aménagement de la forêt riveraine depuis la fin des années 1970, en partenariat avec les agences gouvernementales, les universités et les compagnies membres. D'excellents progrès ont été réalisés en matière de documentation des fonctions écologiques des bandes riveraines et en matière de développement de BPF qui réduisent considérablement les impacts des opérations forestières sur la qualité de l'eau. Aujourd'hui, le débat scientifique et réglementaire au sujet de l'aménagement de la forêt riveraine sur la côte nord ouest du Pacifique se concentre sur la capacité des MPAF et des méthodes de rechange à être efficaces pour la conservation d'aspects importants de la diversité biologique, incluant les espèces menacées d'extinction et/ou hautement sensibles aux perturbations.

Ce rapport brosse un tableau des dernières informations scientifiques et opinions d'experts sur l'aménagement de la forêt riveraine et ses effets sur la diversité biologique de la côte nord ouest du Pacifique. NCASI a donné le mandat au docteur Daniel Sarr du service des Parcs Nationaux d'organiser une équipe de rédaction multidisciplinaire et d'assumer la direction générale du projet. Le docteur Larry Irwin, gestionnaire du Programme de la faune de l'Ouest de NCASI, a travaillé en collaboration avec le docteur Sarr sur la conception du projet et la rédaction de ce rapport.

Dans la partie 1 du rapport, les auteurs principaux discutent de la signification du concept parfois mal utilisé de biodiversité. Ils décrivent comment les processus naturels de perturbations créent l'hétérogénéité de l'habitat qui, à plusieurs niveaux, assure la biodiversité. Même s'il est possible de faire la distinction entre les perturbations forestières et les perturbations naturelles, les auteurs décrivent comment ces deux éléments peuvent être évalués en termes de leurs effets sur la biodiversité, en établissant comment ils influencent l'hétérogénéité de l'habitat, de même que les legs biologiques, les contraintes physiologiques et la disponibilité des ressources. Ces facteurs peuvent être évalués ensembles par l'intermédiaire d'un modèle graphique développé par les auteurs.

Dans la partie 2, le rapport couvre les effets de l'aménagement forestier sur des éléments spécifiques de la biodiversité. Cette information est présentée sous forme de sections préparées par des experts et porte sur plusieurs groupes taxonomiques d'organismes aquatiques et terrestres.

Dans la partie 3, les auteurs principaux présentent une synthèse de l'information spécifique aux taxons et ils proposent quelques principes généraux et approches pour protéger la biodiversité riveraine. Ces éléments peuvent être utilisés à l'échelle du peuplement ou du paysage. À cet effet, les auteurs notent qu'on a récemment porté beaucoup d'attention sur l'approche qui consiste à faire en sorte que les traitements forestiers émulent, autant que faire se peut, les régimes de perturbation naturelle dans les paysages. Cette approche est considérée comme étant la meilleure jusqu'à maintenant, toutefois, elle peut s'avérer non rentable ou encore non réalisable dans certains paysages. La revue fait également ressortir qu'il existe des avantages et des limites à l'approche de bande tampon riveraine en ce qui concerne la protection de la biodiversité. Les auteurs identifient les principales lacunes dans l'information écologique traitant de ce sujet et le rapport conclut en proposant un programme de recherche et un cadre d'évaluation critique des travaux de recherche passés.

L'information, l'interprétation et les recommandations émises par les auteurs de ce rapport entraînent d'importantes implications sur l'établissement des priorités de NCASI. Par exemple, il semble clair que la perception des impacts de la foresterie sur la biodiversité est influencée, en bonne partie, par les pratiques historiques (par exemple, la récolte sans MPAF) de même que par les études spécifiques au niveau du peuplement dont l'applicabilité aux pratiques actuelles et les effets au niveau du paysage sont limités.



Ronald A. Yeske

Octobre 2005

RIPARIAN ZONE FOREST MANAGEMENT AND THE PROTECTION OF BIODIVERSITY: A PROBLEM ANALYSIS

TECHNICAL BULLETIN NO. 908
OCTOBER 2005

ABSTRACT

This report evaluates the general effects of forestry practices on biodiversity along streams in the Pacific Northwest and northern California. There are four parts to the report. In Part I, we present concepts of biodiversity and the processes underlying it. Biodiversity is expressed as a general concept for species, habitat, and genetic diversity of all groups of organisms. We describe the interacting processes that govern riparian biodiversity by integrating those operating over large spatial extents, such as climate, with interrelated ones that have more localized influences, such as disturbance and habitat heterogeneity. The effects of forestry on biodiversity are then analyzed in the context of these controls, and how they are influenced by disturbances. We predict that habitat heterogeneity and retention of pre-disturbance biological legacies (trees, snags, logs, seed and spore banks that can be important to growth of populations of organisms after disturbance) are two of four key determinants of biodiversity because they may act as mechanisms that promote species coexistence. Habitat heterogeneity is especially scale-dependent. Physiological stress and related resource availability are the other two primary controllers of biodiversity because they may limit the number of species that coexist. These limiting factors are strongly influenced by geography. All four factors are combined into a simple graphical model for predicting how disturbance regimes in general, and forestry practices in particular, will affect biodiversity. Disturbance regimes that are intermediate in influence are predicted to best maintain biodiversity. Geographic variation, as described in Appendices A and B, must be considered when implementing the conceptual model, and we illustrate this by contrasting how a variety of forestry practices are predicted to affect biodiversity in relative extremes in the Pacific Northwest: wet forests west of the Cascades vs. dry forests on the east slope of the range.

The primary controllers of species diversity will have different effects on organisms depending on their life histories. Therefore, in Part II, we provide separate chapters by selected authors summarizing information about the effects of forestry practices on biodiversity along streams in the study area for specific taxonomic groups. These summaries contain the most current information on the ecology of the taxonomic groups, and how they and their habitats may be affected by forestry practices. Each section also suggests forestry practices that may sustain the selected taxonomic group. Finally, research needed to improve understanding of these taxa-specific topics is described.

Synthesizing this information in Part III, we stress that there may be tradeoffs in managing for different elements of biodiversity, which leads to complications in managing for overall biodiversity. This highlights the need for clear articulation of management goals. For improving overall biodiversity maintenance, the principles outlined in Part I lead to potentially cost-effective stand-level management actions. In terms of enhancing habitat heterogeneity, planting multiple crop species, leaving some native trees unharvested to remain through a second rotation, lengthening rotations and earlier thinning schedules may all be effective, depending on the circumstances. Woody debris and snags are critical habitat features for many species that can be maintained or created to improve legacy retention. Site preparation following harvesting that creates biological legacies that occur with natural disturbances and that conserves coarse woody debris can help maintain many non-crop species. Controlling exotic species that act as artificial keystones/pest plants can reduce physiological stress and maintain more natural resource availability for native species. We also describe strategies for

maintaining biodiversity at the landscape scale. Specifically, we discuss some advantages and limitations of disturbance regime-based management, riparian buffers, and conservation reserves as means to protect biodiversity.

The report concludes in Part IV with a draft research agenda to complement taxon-specific research recommended in Part II. This research agenda is based on reviews of existing literature and ongoing research, which exhibits geographic and taxonomic biases. The goal of the research proposed is to improve understanding of how to protect biodiversity in managed forests. There is a need for much basic ecological information about both the ecology of lesser known riparian taxa, as well as applied research determining their sensitivity to forestry related disturbance.

KEYWORDS

aquatic invertebrates, biodiversity, birds, buffer, disturbance regime, endangered species, fish, forest zones, fungi, keystone species, mammals, plants, riparian, stream amphibians, vegetation

RELATED NCASI PUBLICATIONS

Technical Bulletin No. 885 (August 2004). *Managing elements of biodiversity in sustainable forestry programs: Status and utility of NatureServe's information resources to forest managers.*

Technical Bulletin No. 857 (January 2003). *Wildlife and biodiversity metrics in forest certification systems.*

Technical Bulletin No. 799 (January 2000). *Riparian vegetation effectiveness.*

Technical Bulletin No. 775 (January 1999). *Assessing effects of timber harvest on riparian zone features and functions for aquatic and wildlife habitat.*

AMÉNAGEMENT FORESTIER DES BANDES RIVERAINES ET PROTECTION DE LA BIODIVERSITÉ : ANALYSE DE LA PROBLÉMATIQUE

BULLETIN TECHNIQUE NO. 908
OCTOBRE 2005

RÉSUMÉ

Ce rapport évalue les effets généraux des pratiques forestières sur la biodiversité le long des cours d'eau de la côte nord ouest du Pacifique et de la Californie du Nord. On retrouve quatre parties dans ce rapport. Dans la partie 1, nous présentons les concepts de biodiversité et ses processus sous jacents. La biodiversité se définit comme un concept général pour les espèces, l'habitat et la diversité génétique de tous les groupes d'organismes. Nous décrivons les processus interactionnels qui gouvernent la biodiversité riveraine en intégrant ceux qui opèrent sur de grandes étendues spatiales telles que le climat, en incluant ceux qui sont interreliés et qui produisent des influences plus locales telles que les perturbations et l'hétérogénéité de l'habitat. Les effets de la foresterie sur la biodiversité sont ensuite analysés selon ces contrôles et selon la façon dont les perturbations les influencent. Nous prévoyons que l'hétérogénéité de l'habitat et la rétention des legs biologiques avant perturbation (arbres, chicots, billes, amas de graines et de spores qui peuvent s'avérer importants pour la croissance des populations d'organismes après perturbation) constituent deux des quatre facteurs déterminants de la biodiversité parce qu'ils peuvent agir comme des mécanismes qui favorisent la coexistence d'espèces. L'hétérogénéité de l'habitat est particulièrement dépendante de l'échelle. La contrainte physiologique et la disponibilité des ressources associées constituent les deux autres agents primaires de contrôle de la biodiversité car ils peuvent limiter le nombre d'espèces qui coexistent. La géographie influence fortement ces facteurs limitants. On a combiné ces quatre facteurs dans un modèle graphique simple pour prédire comment les régimes de perturbation en général et les pratiques forestières en particulier, affecteront la biodiversité. On prévoit que les régimes de perturbations dont l'influence demeure intermédiaire seront les meilleurs pour maintenir la biodiversité. Il est nécessaire de considérer la variation géographique, décrite dans les annexes A et B, lors de l'implantation d'un modèle conceptuel et nous illustrons ceci en comparant comment une variété de pratiques forestières affecteront, on suppose, la biodiversité dans les extrémités relatives de la côte nord ouest du Pacifique : les forêts humides de l'ouest des Cascades vs les forêts sèches le long de la pente est de la chaîne.

Les agents de contrôle primaires de la diversité des espèces produisent des effets différents sur les organismes, dépendant de leurs cycles biologiques. Par conséquent, nous présentons, dans la partie II, des chapitres préparés par des auteurs sélectionnés, qui font la synthèse de l'information sur les effets des pratiques forestières sur la biodiversité le long de cours d'eau situés dans la zone d'étude pour des groupes taxonomiques spécifiques. Ces synthèses contiennent l'information la plus récente sur l'écologie des groupes taxonomiques ainsi que sur la façon dont ces groupes et leurs habitats peuvent être affectés par les pratiques forestières. Chaque section contient également des suggestions sur les pratiques forestières qui sont susceptibles de maintenir le groupe taxonomique retenu. Enfin, on retrouve une description des besoins de recherche pour améliorer notre compréhension des taxons spécifiques.

Nous avons fait la synthèse de cette information dans la partie III et nous mettons l'accent sur le fait qu'il pourrait être nécessaire de faire des compromis dans la gestion des différents éléments de la biodiversité, ce qui amène des complications dans la gestion de la biodiversité globale. Cette situation démontre qu'il est nécessaire de bien formuler les objectifs d'aménagement. Afin d'améliorer le maintien de la biodiversité globale, nous croyons que les principes avancés dans la

partie I sont précurseurs d'actions d'aménagement, au niveau du peuplement, potentiellement rentables financièrement. En ce qui a trait à l'amélioration de l'hétérogénéité de l'habitat, planter de multiples espèces cultivées, laisser quelques arbres indigènes en place jusqu'à une seconde révolution des peuplements, rallonger les périodes de révolution et raccourcir les programmes d'éclaircies représentent toutes des pratiques potentiellement efficaces, selon les circonstances. Les débris ligneux et les chicots demeurent des composantes critiques de l'habitat pour plusieurs espèces et il est possible de les maintenir ou les créer afin d'améliorer les legs biologiques. La préparation des sites après la récolte, qui crée des legs biologiques survenant de concert avec les perturbations naturelles et permettant de conserver les débris ligneux grossiers, est susceptible d'aider à maintenir les espèces non cultivées. Le contrôle des espèces exotiques qui agissent comme plantes essentielles et/ou nuisibles peut réduire la contrainte physiologique et maintenir plus de ressources naturelles pour les espèces indigènes. Nous décrivons également les stratégies pour maintenir la biodiversité à l'échelle du paysage. En particulier, nous examinons certains avantages et certaines limites de l'aménagement basé sur les régimes de perturbations, les bandes riveraines tampons et les réserves de conservation en tant que moyens pour protéger la biodiversité.

Dans la partie IV, le rapport conclut en présentant un programme de recherche préliminaire pour compléter les recherches sur les taxons spécifiques recommandées à la partie II. Ce programme de recherche se fonde sur les revues de la littérature existante et sur les recherches en cours (qui comportent des biais géographiques et taxonomiques). L'objectif de la recherche proposée est d'améliorer la compréhension des moyens pour protéger la biodiversité dans les forêts aménagées. Il existe un besoin d'obtenir plus d'information écologique de base sur l'écologie des taxons riverains et il existe également un besoin en matière de recherche appliquée pour déterminer leur sensibilité envers les perturbations reliées à l'aménagement forestier.

MOTS CLÉS

Invertébrés aquatiques, biodiversité, oiseaux, tampon, régime de perturbation, espèces menacées d'extinction, poissons, zones forestières, champignons, espèces pivots ou essentielles, mammifères, plantes, bande riveraine, amphibiens aquatiques, végétation

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Bulletin technique no. 885 (août 2004). *Managing elements of biodiversity in sustainable forestry programs: Status and utility of NatureServe's information resources to forest managers.*

Bulletin technique no. 857 (janvier 2003). *Wildlife and biodiversity metrics in forest certification systems.*

Bulletin technique no. 799 (janvier 2000). *Riparian vegetation effectiveness.*

Bulletin technique no. 775 (janvier 1999). *Assessing effects of timber harvest on riparian zone features and functions for aquatic and wildlife habitat.*

CONTENTS

PART I PRINCIPLES AND CONCEPTS.....	1
1.0 INTRODUCTION	1
1.1 Purpose	1
1.2 The Concept of Biodiversity.....	1
1.3 Complexity of Riparian Areas	2
2.0 FACTORS CONTROLLING RIPARIAN BIODIVERSITY	3
2.1 Abiotic Processes and Physiological Controls.....	3
2.2 Biotic Processes and Resource Availability.....	4
2.3 Disturbance Processes.....	4
3.0 CONCEPTUAL MODELS OF DISTURBANCE AND SPECIES DIVERSITY	7
3.1 Habitat Heterogeneity, Biological Legacies, and Biodiversity Predictions.....	9
3.2 Intensity, Frequency, and Size of Disturbances.....	10
4.0 A CONCEPTUAL MODEL FOR EVALUATING DISTURBANCE EFFECTS ON BIODIVERSITY	12
4.1 Linking Effects of Geographic Variation... ..	13
4.2 Evaluating the Effect of Riparian Forest Management across the Pacific Northwest.	14
5.0 POLICIES FOR PROTECTING RIPARIAN AREAS.	16
PART II TAXA-SPECIFIC INFORMATION	17
6.0 FORESTRY PRACTICES AND AQUATIC BIODIVERSITY.....	18
6.1 Fish (by Robert E. Gresswell).....	18
6.2 Stream Amphibians (by R. Bruce Bury).....	23
6.3 Macroinvertebrates (by Nicole M. Czarnomski)	27
7.0 FORESTRY PRACTICES AND TERRESTRIAL BIODIVERSITY	32
7.1 Vascular Plants (by Robert J. Pabst and Daniel A. Sarr).....	32
7.2 Non-Vascular Plants (by Jeff Shatford).....	38
7.3 Fungi (by Daniel A. Sarr)	42
7.4 Mammals (by Jennifer M. Weikel).....	44

7.5	Birds (by Jennifer M. Weikel).....	49
7.6	Invertebrates (by Andrew R. Moldenke).....	53
8.0	KEYSTONE AND ENDANGERED SPECIES.....	58
8.1	Keystone Species and Concepts.....	58
8.2	Rare, Sensitive, and Endangered Species.....	59
PART III APPROACHES FOR PROTECTING RIPARIAN BIODIVERSITY		60
9.0	SYNTHESIS AND SUMMARY OF TAXA-SPECIFIC RESPONSES	60
9.1	Effects on Aquatic Biodiversity	60
9.2	Effects on Terrestrial Biodiversity	61
10.0	STAND-SCALE APPROACHES FOR PROTECTING BIODIVERSITY	62
11.0	MULTISCALE MANAGEMENT APPROACHES FOR PROTECTING BIODIVERSITY ..	64
11.1	Modeling Management after Natural Disturbance	64
11.2	Riparian Buffers	65
11.3	Reserve-Based Management	67
PART IV PAST, PRESENT, AND FUTURE RESEARCH.....		67
12.0	EXISTING LITERATURE AND ONGOING RESEARCH.....	67
13.0	A MEANS FOR ASSESSING RIPARIAN LITERATURE.....	71
14.0	A RESEARCH AGENDA TO SUPPORT RIPARIAN BIODIVERSITY PROTECTION	72
14.1	Programmatic Recommendations.....	72
REFERENCES		78
APPENDICES		
A	Forest Zones in the Pacific Northwest.....	A1
B	Disturbance Regimes in Riparian Areas of the Pacific Northwest.....	B1

TABLES

Table 4.1	Effects of Different Forest Management Options on the Fundamental Drivers of Biodiversity and Their Relative Potential for Maintaining Biodiversity in 30-60-Year-Old, Second Growth Riparian Forest Landscapes on the Wet Temperate West Side (W) and Xeric East side (E) of the Cascades.....	15
Table 7.1	Riparian Obligate Species of Mammals in Coniferous Forests of the Pacific Northwest (Anthony et al. 2003)	45
Table 7.2	Riparian-Associated Species of Mammals in Coniferous Forests of the Pacific Northwest (adapted from Anthony et al. 2003).....	45

FIGURES

Figure 2.1	Hypothesized Disturbance Regime for a 500-Hectare Riparian Forest.	6
Figure 3.1	Relationship between Disturbance Frequency and Species Diversity (Connell 1978).....	7
Figure 3.2	Species Diversity as a Function of Disturbance Frequency or Intensity and Competitive Displacement (Huston 1979).....	8
Figure 4.1	Conceptual Model for Evaluating How Forestry Disturbance Is Predicted to Influence Biodiversity	12
Figure 4.2	Conceptual Relationship between Local Riparian Vascular Plant Species Richness and Site Productivity at Riparian Forest Sites across the State of Oregon	13
Figure 4.3	Relative Importance of Disturbance Effects on Factors Affecting Species Diversity in Sub-Regions of the Pacific Northwest.....	14
Figure 12.1	Number of Ongoing Studies by Taxonomic Group Identified in the Forest Research Database.....	69
Figure 12.2	Number of Ongoing Studies by Taxonomic Group Identified in the University of Washington/Rocky Mountain Research Station Bibliography	70
Figure 12.3	Number of Ongoing Studies by Geographic Area Identified in the Forest Research Database.....	70
Figure 14.1	Conceptual Model of Controls on Biodiversity, and Roles of Inventory, Monitoring, and Research.....	73
Figure 14.2	Three Potential Response Curves for Lichen Diversity as a Function of Green Tree Retention.....	76
Figure 14.3	Conceptual Models of Physiological Stress and Recovery in a Riparian System (based on Sarr 2002).....	77

RIPARIAN ZONE FOREST MANAGEMENT AND THE PROTECTION OF BIODIVERSITY: A PROBLEM ANALYSIS

PART I PRINCIPLES AND CONCEPTS

1.0 INTRODUCTION

1.1 Purpose

In this report, we outline broad principles, information needs, and research directions to support biological diversity protection in riparian forests on private lands of the Pacific Northwest. We addressed the complex topic of riparian biodiversity by recognizing that a small set of key processes primarily structure ecosystems and their biological organization (Holling 1992). Primary controls on the biological diversity that can exist in a given area have been identified through literature review and critical analysis by the authors for their relevance to Pacific Northwest riparian forests and their potential application across taxa. These controls are habitat heterogeneity, legacy retention, physiological stress, and resource availability. We incorporate these into a simple graphical model for evaluating effects of disturbance regimes, including forestry practices, on biodiversity in general. Use of the model requires an understanding of how a particular disturbance affects these four variables. This will be influenced by regional climate and other factors that vary spatially; therefore, we describe important aspects of geographic variation in the Pacific Northwest (summarized in Appendices A and B). We illustrate how this geographic variation influences disturbance effects by comparing how several standard forestry disturbances would be predicted to affect biodiversity in wet temperate forests west of the Cascades vs. those forests found on the xeric eastside of these mountains. Because there are tradeoffs in managing for different elements of biodiversity, we also provide an analysis of the effects of forestry practices on different life history groups. Individual authors present short chapters summarizing biology for each group, followed by a discussion of documented or expected responses of each group to riparian forest management.

The question of how best to maintain biodiversity is complex, involving social as well as ecological concerns. We will not address these broader societal questions. Instead, our intent is to provide a sufficient framework for evaluating the effects of various forestry approaches on overall biodiversity, and to recognize where differential responses among elements of biodiversity will occur. In addition, we conclude the report by providing a research agenda to better inform riparian biodiversity conservation on private lands in the Pacific Northwest. Although we articulate general principles that will be applicable in most forests, our particular study area is the Pacific Northwest portion of Washington, Oregon, and California, extending eastward to the east slope of the Cascades.

1.2 The Concept of Biodiversity

Biodiversity is a general concept for species, habitat, and genetic diversity of all forms of life (Westman 1990; Hunter 1999). Diversity embodies the amount of all three per unit area (e.g., species richness), their equitability (evenness in relative abundance) (Whittaker 1975; Westman 1990), and maintenance of viable populations of a complete array of native species. Compositional, structural, and functional biodiversity have also been recognized (Roberts and Gilliam 1995). Much of the focus, in the literature and here, is on compositional biodiversity (species assemblages). Biodiversity protection may or may not be consistent with maximizing species richness at a given, particularly local, scale. Instead, it is about preventing biological impoverishment at multiple levels of organization.

Unfortunately, there may be no metric that tracks trends in biodiversity and works well for the wide range of settings or life forms occurring in natural landscapes (reviewed by Layton, Guynn, and Guynn 2003; NCSSF 2005). The occurrence or absence of certain species, groups of species, or other biophysical elements may all be indicators of the status of biodiversity. Loss of any species may be an important, simple indication of degradation of overall biodiversity, particularly if the species is one that regulates the abundance of others (e.g., keystone, symbiotic, or mutualistic species). Conversely, return of a species extirpated in the past may be an important, simple indication of recovering biodiversity. However, both extirpation of species or addition of species (via normal dispersal) in a given area can be unrelated to biodiversity trends or to management actions. Such contrasts are inherent in the dynamic nature of populations, as well as processes underlying biodiversity in riparian areas, complicating the analysis of forest management effects on biodiversity.

Non-equilibrium processes and population dynamics over variable spatial and temporal scales must be considered when addressing questions about biodiversity protection (Spies and Turner 1999; NCSSF 2005). Changes in climate, human land use, and management lead to non-equilibrium dynamics. For example, vegetation at a given location changes over time and so does the nature of its biodiversity. At certain scales, a landscape is composed of few to many units that may be in the same (large disturbance events) or different (small disturbance events) developmental stages. Biodiversity at scales larger than the stand is determined by how disturbance events are synchronized or otherwise juxtaposed at these larger scales. This is particularly complicated in riparian forests.

1.3 Complexity of Riparian Areas

Riparian areas are among the biosphere's most complex environments (Naiman, Bilby, and Bisson 2000). They possess distinct ecological characteristics resulting from the interaction between terrestrial and aquatic ecosystems (Gregory et al. 1991; Naiman, Bilby, and Bisson 2000). From a functional perspective, riparian areas are considered to extend outward from the stream channel to the limits of flooding or beyond (Gregory 1997) and upward to include the canopy of streamside vegetation (Swanson et al. 1982). The steep environmental gradients, dynamic nature, and geomorphic complexity in riparian areas combine to support a great abundance and variety of life (Naiman et al. 1992). Riparian areas can have a disproportionate effect on ecosystem processes through their influence on water quality, terrestrial wildlife, primary productivity, and aquatic food webs (Gregory et al. 1991; Naiman et al. 1992; Minore and Weatherly 1994). Forestry practices can modify the biophysical dynamics and thus biodiversity in riparian areas (Brinson and Verhoeven 1999).

1.3.1 Riparian Forests of the Pacific Northwest

Appendix A describes general riparian and associated upland vegetation in forestlands and how it varies across the study area. Major vegetation types recognized by Franklin and Dyrness (1988) for Washington and Oregon, and Barbour and Major (1977) for California, are summarized and dominant species listed. The zones recognized by Franklin and Dyrness (1988) apply northward into British Columbia and southeast Alaska. Only forests from the northwest corner of California, the Klamath region, are included; the remainder of the state is not considered to be in the Pacific Northwest.

A general trend in riparian and associated upland vegetation is an increasing contrast between the two along the gradient from wet coastal forests to the drier inland forest in the Klamath region and the eastside of the Cascades (Appendix A). This east-west geographic variation will be discussed throughout this report, particularly in terms of how it affects physiological stress and resource availability following disturbance.

2.0 FACTORS CONTROLLING RIPARIAN BIODIVERSITY

In large and complex regions such as the Pacific Northwest, a multi-scale hierarchy of controls governs the distributions of organisms in time and space (Bestelmeyer, Miller, and Wiens 2003; Sarr, Hibbs, and Huston 2005). Climate, topography and other abiotic factors impose the broadest controls on resource availability and physiological stress, which in turn are influenced by biological interactions. Resource availability is defined as the presence of growth resources such as mineral nutrients, light, and growing space that allow species establishment and growth. Stress has been defined generally as the physiological response of an individual, or the functional response of a system caused by disturbance or other ecological process relative to a reference condition. It is characterized by direction, magnitude, and persistence (Rykiel 1985). Understanding the effects of disturbance on physiological stress and resource availability is key to predicting the responses of biodiversity to forestry practices. Habitat heterogeneity and biological legacies left in the wake of disturbance are two additional keys to understanding this response.

2.1 Abiotic Processes and Physiological Controls

Temperature and moisture conditions provide the most fundamental constraints on organisms through their direct effects on photosynthesis, metabolism, net primary productivity, and other physiological processes whose limits govern species' distributions. These processes underlie vegetation formations at the broadest scales (Holdridge 1947; Sarr, Hibbs, and Huston 2005) and affect the distributions of animals as well (Currie 1991; Hansen and Rotella 1999). Variation and interaction among temperature, humidity, and radiation in both space and time are also important factors driving the developmental or reproductive biology of many species.

Climatic gradients in the Pacific Northwest are the steepest in North America (Franklin and Dyrness 1988), and field and modeling studies have demonstrated that many elements of forest ecosystems vary across the gradients, including vegetation composition (Ohmann and Spies 1998, Appendix A), canopy density (Grier and Running 1977), primary productivity and ratios of above to below ground biomass (Runyon et al. 1994). Riparian plant diversity and composition show corresponding variation across climate gradients in the Pacific Northwest (Pabst and Spies 1998, 1999) as well as predictable, directional species responses to climate-driven variation in disturbance (Sarr 2005). Climate and its interaction with other large-scale landscape characteristics such as environmental or evolutionary history may therefore be viewed as a primary set of controls on spatial patterns of riparian biodiversity. Such geographic controls are fundamental to understanding effects of forest management at different locales (see Sections 4.2 and 4.3).

At more local scales, variation in geology, topography, and other watershed characteristics form a secondary set of abiotic controls on species distributions. For example, Whittaker (1960) and Harrison, Viers, and Quinn (2000) observed that vascular plant species turnover with change in elevation (Beta diversity) occurred more rapidly on serpentine vs. granitic or other substrata. At the basin scale, variation in geomorphology, hydrology, and soils create a varied template for riparian and aquatic biodiversity (Leopold, Wolman, and Miller 1964; Swanson et al. 1988). Gradients in climate, stream power, and channel gradient from headwaters downstream provide habitat heterogeneity that differentiates the riparian vegetation in any given watershed (Hupp 1986; Gregory et al. 1991; Tabacchi et al. 1996). At the stream reach scale (10's to 100's of meters), such abiotic factors result in steep gradients in factors influencing physiological stress, such as microclimate and soil oxygenation, and resources such as soil moisture. These gradients further differentiate riparian areas. Physical variability in the environment fosters complexity in vegetation composition and structure, yielding distinctive habitat for other life forms.

2.2 Biotic Processes and Resource Availability

At the scale of a riparian forest stand or stream reach, biotic processes become key controls on biodiversity. Biotic processes that result in pulses of nutrients and/or available light have an important influence on resource availability (Pollock, Naiman, and Hanley 1998). Biotic processes structuring vegetation increase habitat heterogeneity by creating more vertically, horizontally, and compositionally complex vegetation (MacArthur and MacArthur 1961; Moran 1980). Interactions among organisms, such as disease-mediated interactions and competition for limited resources, are key biotic processes affecting local diversity. Diseases caused by exotic pathogens may cause atypically high mortality, leading to local extinction, for example, the root rot (*Phytophthora lateralis*) to which Port Orford cedar has no natural resistance (Hansen et al. 2000; Jules et al. 2002). Non-native diseases can act as artificial keystone species (see Section 8.1) not only by having such strong pathogenic effects, but also by their competitive ability to displace native species (Elton 1958). Similarly, large vertebrate consumers with low population sizes are especially vulnerable to displacement and have been lost from many environments even where suitable habitat may exist (Duffy 2003). Such vulnerability appears to be trophically mediated, with important implications for conservation.

Competition among native species is perhaps the most important biological regulator of local diversity. It is the process that leads to dominance/equitability relationships that in turn affect the number of species that can coexist in an area (Whittaker 1975). In many cases, competition among similar functional groups of species is strongly linked to resource availability, with resource-rich environments fostering intense interspecific competition (Huston 1994). The factors that increase or decrease the rates of competitive exclusion, especially disturbance, are integral to models of diversity described in Section 3.0.

2.3 Disturbance Processes

Disturbance may be defined as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Pickett and White 1985). Riparian forests are influenced by the most complex disturbance regimes in the Pacific Northwest, juxtaposing mass failure, fluvial, ice, fire, gap, herbivore, and pathogen-mediated disturbances (Gregory et al. 1991; Pollock, Naiman, and Hanley 1998; Naiman, Bilby, and Bisson 2000). Disturbance affects resource availability and physiological stress directly. Disturbances of variable area, frequency, and intensity also enhance habitat heterogeneity and regulate the dominance of highly competitive species, reducing competitive exclusion. Both effects will tend to increase diversity (Huston 1994; Spies and Turner 1999, Section 3.0). The two effects also partially explain why riparian areas usually have higher diversity than adjacent uplands. Finally, the maintenance of many species across cycles of disturbance requires persistence of biological legacies such as regeneration propagules (Odion and Davis 2000), or resources such as woody debris (Lindenmayer and Franklin 2002).

There is a developing conceptual framework for riparian ecosystems in the Pacific Northwest whereby geophysical disturbances, driven by direct and indirect abiotic effects, establish a dynamic mosaic of surfaces (e.g., channels, channel units, floodplains, terraces, alluvial fans) that may act as a template for riparian biodiversity (Grant and Swanson 1995; Fetherston, Naiman, and Bilby 1995; Swanson et al. 1988; Pollock, Naiman, and Hanley 1998; Johnson, Swanson, and McGee 2000). The importance of different geophysical disturbances changes with stream order and channel gradient. Along larger streams flooding is more important; at headwater streams, landslides and debris flows dominate (Montgomery 1999). These processes operate at time scales ranging from months to years for chronic disturbances such as flooding to decades or centuries for episodic events such as debris flows. Likewise, spatial scales range from local to landscape-wide.

The fluvial/mass movement processes that structure riparian areas are controlled by basin geology, hydrology, and inputs of inorganic and organic material from adjacent slopes (Gregory et al. 1991). In the Pacific Northwest, large, infrequent landslides may play a dominant role in distributing woody debris from upland areas to streams (Reeves et al. 1995). The importance of large wood as a habitat feature supporting a number of elements of biodiversity has been well established in this region (Harmon et al. Franklin 1986; Naiman, Bilby, and Bisson 2000; Johnson et al. 2000). The template for biodiversity created by these geophysical disturbances is heterogeneous in geomorphology, soils, and vegetation composition and structure (Gregory et al. 1991; Pollock, Naiman, and Hanley 1998).

Fire will also directly and indirectly influence the riparian biodiversity template. Runoff and sedimentation processes increase after fire as a function of fire severity, the proportion of a watershed that burns, and post-burn rainfall patterns (Swanson 1981). Fire removes litter and vegetation in direct proportion to its severity. In addition, high severity fire can increase water repellency and decrease root strength. Increases in sedimentation with fire are caused by not only mass soil movements, but also by surface erosion processes (McNabb and Swanson 1990). Fire-induced tree mortality creates woody debris that is readily transported downslope by fluvial and mass movement events that occur more frequently following fires (Swanson et al. 1987; McNabb and Swanson 1990). These processes, and increased summer streamflows that often follow fire, both have a variety of effects on aquatic species.

Within riparian areas in the Pacific Northwest, considerable uncertainty exists about more direct effects of fire due to a lack of fire history information specific to streamside areas (reviewed by Dwire and Kauffman 2003). Recent studies in the Klamath region and eastern Cascades have found that fire return intervals in riparian reserves are more variable than in adjacent uplands and tend to be longer (Poage 1994; Everett et al. 2001; Skinner 2003). By acting as occasional barriers to fire spread, riparian areas may enhance the spatial and temporal diversity at the watershed scale. However, under favorable conditions for combustion, fire may readily spread through riparian areas as shown by physical evidence of continuity in fire disturbance among riparian areas and uplands on both sides (Poage 1994; Everett et al. 2001). Weather, fuel moisture, width of stream, topography, orientation of riparian areas relative to prevailing wind, fire intensity in upslope areas and other factors will affect the probability of fire crossing over riparian areas (Agee 1993).

Local disturbances that open gaps in the forest canopy are also important in Pacific Northwest forests in terms of affected area over time. Wind, disease, and insects are among the agents that create gaps. Gap creation rates for upslope forests range between 0.2% and 2% of a stand each year, which is equivalent to a rotation period of 50-500 years (Runkle 1985; Spies, Franklin, and Klopsch 1990). Gaps may cover 5-30% of a forest and affect 50% of the area at any given time. These gap-forming disturbances, though believed to be less common in riparian areas than upslope, are nonetheless widespread and are important for local plant diversity and tree regeneration (Sarr 2005). Many animals are also believed to respond to this fine scale heterogeneity in forests, including birds (Section 7.5), mammals (Section 7.4) and invertebrates (Section 7.6).

Wind disturbances also open large patches in forests (Hansen and Rotella 1999; Stinton et al. 2000). For example, in the western Cascades, Stinton et al. (2000) found that 10% of a landscape was affected by windthrow from 1890 through the late 1990s, and that less area was affected per year prior to onset of timber harvest. Climate, landform, stand conditions, and other disturbances, including timber harvest, will increase the frequency of windthrow events.

Figure 2.1 shows the relative frequency of both episodic (fire) and chronic (gap, small floods) disturbances in a hypothetical riparian forest over a 200-year period (episodic debris flows occur over longer time scales in an area this size, Swanson et al. 1987). The general pattern of relatively continuous disturbance of different types illustrates the dynamic nature of riparian areas over

relatively short time scales. In this example, the rotation intervals (time it takes for the whole 500 ha to be affected) for the different disturbances are 80.7, 85.5, 82.8, and 602.4 years for gap, fire, flood, and windthrow disturbances, respectively.

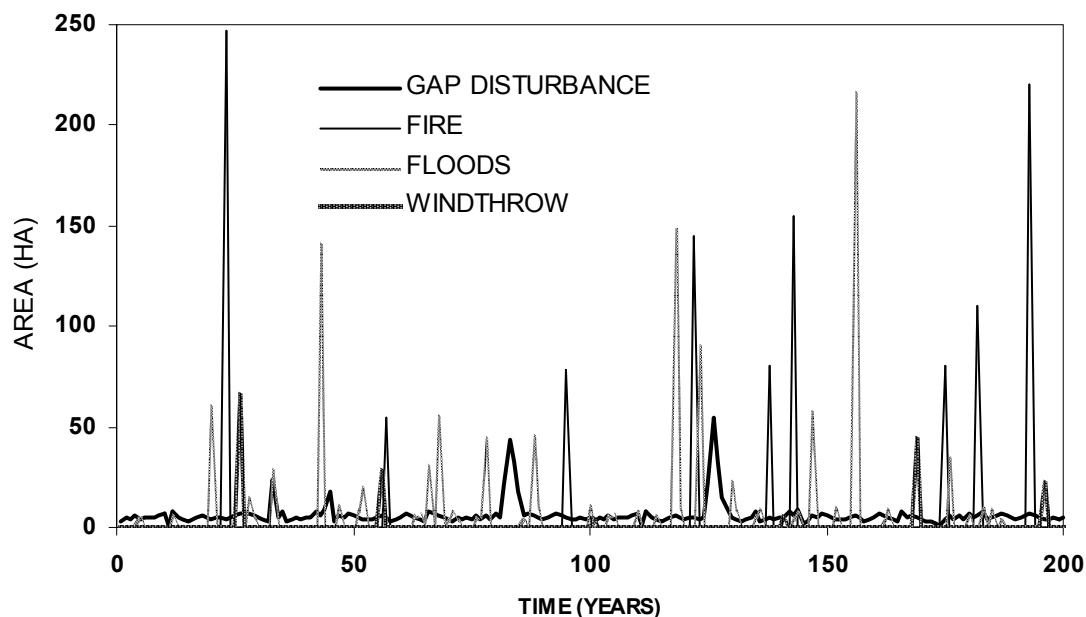


Figure 2.1 Hypothesized Disturbance Regime for a 500-Hectare Riparian Forest Based on Typical Mid-Elevation Disturbance Frequencies in the Study Area (see also Appendix B)

Although a similar degree of *relative* importance in these disturbances is likely to occur in riparian areas over much of the Pacific Northwest, the frequency, severity, and size of disturbances shown in Figure 2.1 all vary considerably across the study area. Understanding variations in natural disturbance regimes of an area can help to predict how forestry practices will interact with and affect biodiversity. In addition, aligning timber harvest disturbances to more closely emulate natural disturbances is an approach for improving biodiversity protection (see Section 11.1). Appendix B summarizes variation in large disturbances in the Pacific Northwest. Managers will need more specific information on their local areas and to keep in mind the points described below.

Fluvial and mass movement processes vary greatly throughout the Pacific Northwest in response to geologic and climatic factors (Swanson et al. 1987). The episodic nature of these disturbances makes their regimes difficult to characterize. A key factor is the potential for significant rain-on-snow events in different areas (Appendix B), which produce especially pronounced peak flows and associated effects.

Figures reported in Appendix B are not from riparian areas, but rather from uplands, which often burn more frequently. Reported figures are based on sampling fire scars on trees, methods whose precision is not well described and which are biased toward more frequent fire and toward surface fire (Baker and Ehle 2001; Whitlock 2004). Between the crown fire systems of higher elevations and the northwest coast, and the open forests of the east side of the Cascades there are complex mixed severity landscapes (Agee 1993), structured by patchy crown fires. The dynamics of these landscapes are poorly understood (Odion et al. 2004). This is made difficult by the variable nature of crown fire occurrences (Turner and Romme 1994).

3.0 CONCEPTUAL MODELS OF DISTURBANCE AND SPECIES DIVERSITY

It is impossible to describe succinctly the effects of disturbances on all aspects of biological diversity simultaneously. Species will show disparate responses to any disturbance given differences in sensitivity to disturbance frequency or intensity, specific requirements for habitat structure, and variation in dispersal and competitive ability. Even these fundamental elements of disturbance response are poorly understood for the majority of species occurring in riparian forests.

Nonetheless, extant conceptual models provide a theoretical foundation for evaluating landscape level species diversity in relation to disturbance. These models have broad empirical and theoretical support. They not only provide a starting point for posing hypotheses of disturbance responses for groups of species, but we use them as a basis for developing our conceptual model for predicting effects of forestry disturbances (Section 4).

According to Connell (1978), ecological communities of sessile organisms are composed of early seral species that colonize quickly after disturbance and late seral species that increase in abundance and dominance with time since disturbance. Maximum diversity occurs, therefore, when disturbance is sufficiently frequent to limit dominance, while allowing ample time for colonization by all species (Connell 1978; Sousa 1979; Petraitis, Latham, and Niesenbaum 1989) (Figure 3.1). Coexistence mechanisms based on the Intermediate Disturbance Hypothesis have been advanced in recent publications (reviewed by Roxburgh, Shea, and Wilson 2004).

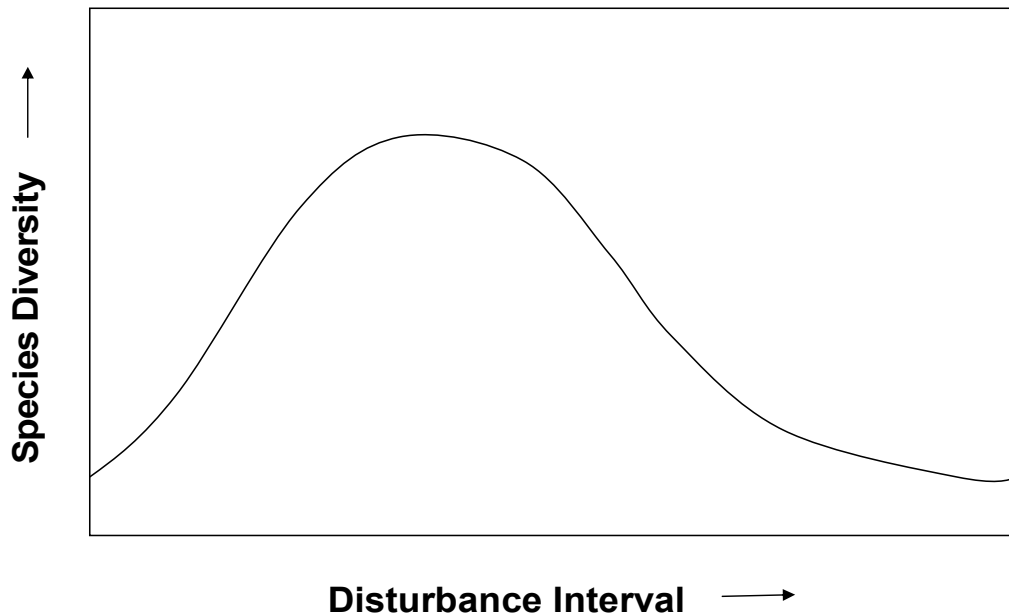


Figure 3.1 Relationship between Disturbance Frequency and Species Diversity (after Connell 1978)

The closely related *Dynamic-Equilibrium Hypothesis* (DEH) of species diversity (Huston 1979) linked the Intermediate Disturbance Hypothesis with observations that species richness is often highest at intermediate productivities (Grime 1973). Huston (1979) proposed that the relationships between disturbance and local diversity depend upon site quality, because competitive exclusion depends upon *both* the disturbance regime and the rate at which dominance develops. The result is a response surface that predicts richness along axes of productivity and disturbance frequency and or intensity showing why diversity varies at the landscape scale (Figure 3.2). The Dynamic-Equilibrium Hypothesis has received empirical support in grassland ecosystems, tropical rainforests, and Pacific Northwest wetlands (Sarr, Hibbs, and Huston 2005)

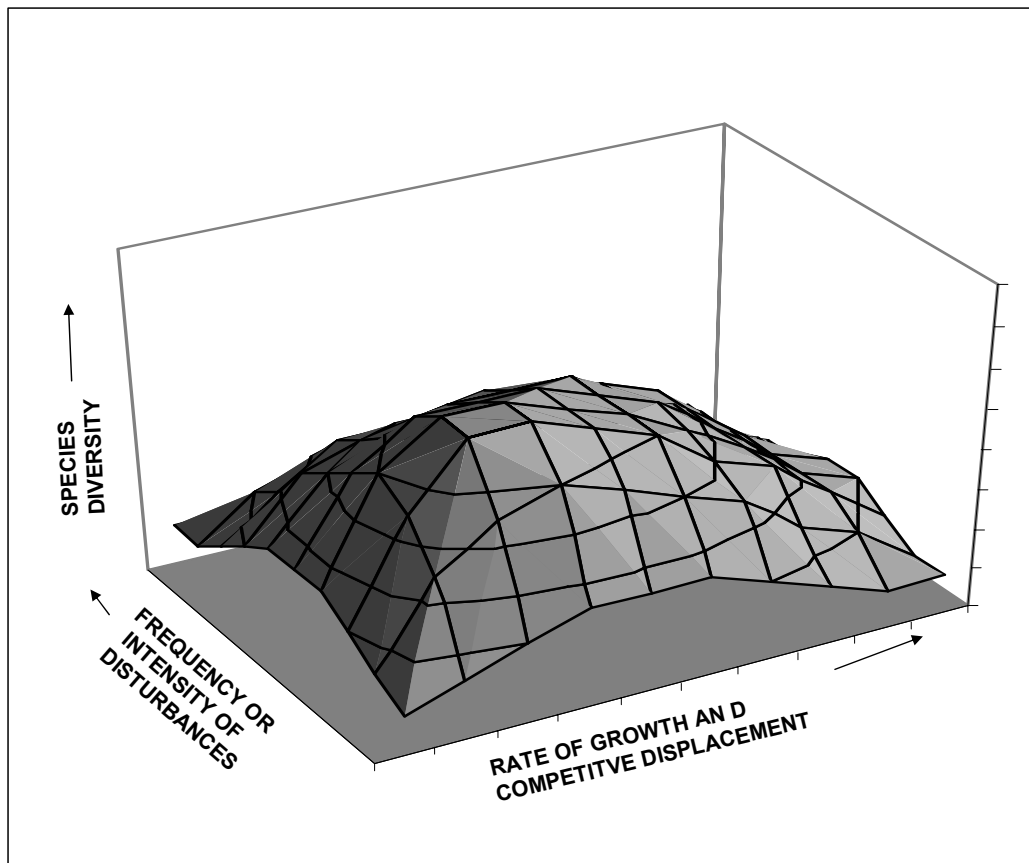


Figure 3.2 Species Diversity as a Function of Disturbance Frequency or Intensity and Competitive Displacement (after Huston 1979) (Rates of growth and competitive displacement are hypothesized to increase with rising site productivity.)

Existing conceptual models of local diversity echo a common theme: there is a relationship between disturbance and diversity, where intermediate levels of disturbance yield highest richness (Sarr, Hibbs, and Huston 2005). The Dynamic Equilibrium Hypothesis is perhaps the most robust model in that it explicitly links productivity to disturbance dynamics. Huston (1999) recognized that the models predicting highest diversity at intermediate levels of disturbance and productivity apply primarily to species within similar functional groups competing for limiting resources (e.g., vascular plants, intertidal organisms, planktonic algae). He speculated that different functional groups would respond distinctively to gradients of productivity and disturbance, with primary producers peaking in

species richness at relatively low levels of productivity, because of the importance of competitive displacement at higher productivity levels. Conversely, species richness in upper trophic levels would be greatest at relatively high levels of ecosystem productivity.

Huston (1994, 1999) further developed these ideas to categorize landscapes by ecosystem productivity and disturbance regime and to recognize inherent differences in the patterns of diversity of distinct life forms. Using the DEH, Huston (1999) distinguished four landscape types involving combinations of high or low productivity and disturbance. In the high productivity, low disturbance scenario, Huston (1999) predicted low landscape heterogeneity due to rapid revegetation following disturbance. He predicted such landscapes would have low vascular plant richness, but possibly high richness of higher life forms, especially sensitive groups of species. An example of this type in the Pacific Northwest might include mesic old growth upland forests. High productivity, high disturbance landscapes should have higher levels of plant richness and relatively high richness of other life forms due to the high heterogeneity maintained by disturbance regimes. Riparian forests would likely fit into this landscape category. In low productivity, low disturbance landscapes, Huston predicted diverse and distinctive plant communities, but relatively low diversity of higher trophic groups. Huston cited tropical rainforests on infertile soils, or semi-arid woodlands as examples of this group. Other examples might include exceptionally infertile sites, such as the distinctive woodlands occurring on serpentine soils. The final landscape type, low productivity, high disturbance is predicted to be a low diversity type for all groups.

Although the DEH provides a powerful general model for predicting species diversity, the model and its derivatives must still be used with caution. It probably applies best for vascular plants (but see Currie 1991); other groups may respond differently than implied by Figures 3.1 and 3.2 (see Section 9), and there is less known about diversity patterns for other groups, particularly fungi, invertebrates, and non-vascular plants. The model also implies that ecosystem productivity and disturbance are the primary factors governing spatial patterns of biodiversity. There is a need to incorporate habitat heterogeneity and biological legacies left after disturbance into biodiversity predictions.

3.1 Habitat Heterogeneity, Biological Legacies, and Biodiversity Predictions

Heterogeneity is a multiscale concept encompassing a tremendous range of physical and biological complexity. Not only does diversity show a positive relationship with habitat heterogeneity (Kerr and Packer 1997; Huston 1994; Roxburgh, Shea, and Wilson 2004), but also viewed across taxa this relationship holds at the full range of scales, making the value of habitat heterogeneity for biodiversity one of the most reliable generalizations in conservation biology. Therefore, we incorporate heterogeneity along with the DEH as an organizing factor in the model we present in Section 4.

The habitat heterogeneity of a riparian forest varies across a range of spatial and temporal scales. The relative importance of such environmental variation is dependent upon the size, mobility, trophic status, and life span of the organism. Where the distribution and abundance of forest bryophytes might respond to fine scale variation in the chemistry or texture of tree bark, an elk herd may be influenced more directly by the much coarser scale patchiness of forest openings at the landscape scale.

Natural disturbance regimes juxtapose complex spatial and temporal patterns of disturbance upon landscapes and create not only an array of competitive environments, but also sharply contrasting abiotic conditions and habitat structures. Thus, physical complexity in environments (see Section 2.1) interacts with temporal variability created by disturbances (Section 2.3) to produce much of the habitat heterogeneity underlying biodiversity. Within forest stands, complexity in vegetation and soils form additional heterogeneity. Generally, old-growth riparian stands, with ongoing tree mortality and establishment, contain the most complex suites of living and dead structures. These include live boles

and branches of different forms, snags, downed logs, deep organic soils with occasional tip-up mounds, densely wooded areas and hardwood-, shrub-, or herb-filled gaps. Although the juxtaposition of compositional and structural characteristic of old forests is believed to be an important template for biological diversity, complexity can also arise from large but incomplete disturbances, such as low to moderate severity fire, pathogen outbreaks, or windthrow that leave patches of living and dead trees, interspersed with disturbed areas of various sizes and degrees of mortality. Many forms of disturbance can positively affect heterogeneity if they are non-uniform in spatial extent, asynchronous in return interval, and variable in intensity.

Indigenous disturbance processes over evolutionary time have given rise to ecosystem resiliency, which is essential for the maintenance of biological diversity. This resilience is caused by natural succession processes that are in turn strongly dependent upon the biological legacies such as green seed trees, large wood, seed and spore banks, and resprouting organs that remain through disturbances (Perry 1994; White and Jentsch 2001; Franklin et al. 2002). Ecosystem recovery and ecological “memory” (the ability to return to a former condition through endogenous properties (Peterson 2002)) can depend entirely on legacies such as seed banks (Odion and Davis 2000). Legacies include resources stored by organisms during favorable conditions, which can be used for growth following disturbance. This “storage effect” has been identified as an important disturbance mediated coexistence mechanism (Warner and Chesson 1985; Chesson 2000; Roxburgh, Shea, and Wilson 2004). These essential functions of stored resources that can survive disturbance make retention of pre-disturbance biological legacies a fundamental consideration for biodiversity maintenance in managed riparian landscapes. Thus, we incorporate legacy retention with habitat heterogeneity, competitive exclusion, and physiological stress as primary factors to consider in evaluating disturbance and diversity relationships.

3.2 Intensity, Frequency, and Size of Disturbances

The Intermediate Disturbance and Dynamic Equilibrium Hypotheses do not provide a framework for evaluating differences in the interrelated nature, scale, and timing of disturbances, and how these may affect legacy retention, habitat heterogeneity, competitive exclusion and stress. Properties of natural disturbance regimes and their interrelated effects have been discussed by Miller (1982) and Malanson (1984). There are gradients in the following disturbance properties that affect the primary controls on biodiversity.

Intensity. Amount and kinds of vegetation killed, growing space made available, and biological legacies that remain. For forestry-related disturbance, this will be a reflection of the amount of existing forest, understory vegetation, forest floor and soil removed by harvests. In terms of forestry disturbances in riparian areas, proximity to stream may be an important component of disturbance intensity because natural disturbance levels are likely to be greater nearest the stream. Disturbance intensity is generally inversely correlated with frequency (Malanson 1984).

Frequency. Amount of time between disturbances. This is often expressed as an average (e.g., mean fire return interval); however, the time between disturbances is often highly variable, and so the range can be more meaningful.

Size. Geographic extent of a disturbance. This will also depend on frequency. Both are needed to calculate the amount of area that will be disturbed over a given time period.

Based on conceptual models of species diversity, disturbance regimes that are intermediate in characteristics may maximize diverse assemblages of species. Therefore, one metric for analyzing biodiversity protection is the extent to which disturbance effects are within the range of intermediacy. Because “intermediate” may imply central tendencies, it is important to emphasize that intermediate disturbance regime management does not require that intensity, size, and frequency each be maintained separately at intermediate or average levels. Relative extremes in disturbances and

stochasticity are often important to coexistence and diversity (Christensen 1991; Gaines and Denny 1993; Clark et al. 2003). Instead, if any one dimension of disturbance, e.g., intensity, is high, the other two would need to compensate (e.g., frequency and size cannot also be high). To maintain intermediacy, intense disturbances can be infrequent and/or small, high frequency disturbances can be small and/or of low intensity, and large disturbances can be infrequent and/or low in intensity (Miller 1982; Malanson 1984). Maintaining biodiversity will be most difficult where two or especially all three disturbance regime properties are outside the bounds of intermediacy.

While the concept of intermediacy in disturbance regimes is a primary nonequilibrium explanation for high levels of diversity, the dimensions of intermediate regimes are qualitative (Shea, Roxburgh, and Rauschert 2004). Intermediate disturbance regimes may approximate those that have historically occurred in terms of balancing intensity, size, and frequency. Thus, explicitly managing based on historic disturbance regimes can be an approach for maintaining an intermediate disturbance regime (Section 11.1). However, historic range of variability is hard to measure, and is dependent on the time frame chosen as a reference. A recent review on biodiversity and sustainable forestry suggests that the historic range of variability concept must be updated and adapted with new information to be useful (NCSSF 2005). Data about climate change, invasive species, fragmentation, and other modern circumstances should be considered. In addition, there is great variability in historic disturbance regimes across the Pacific Northwest (Appendix B). Human impacts have both suppressed and increased disturbance. The entire regime of disturbances, including those of human origin, must be evaluated to determine how biodiversity will be affected. The model presented in Section 4 was prepared for this purpose.

The amount of legacy removal may be one measure of disturbance intensity. It is important to consider relatively apparent disturbance effects to aboveground legacies as well as less apparent effects to litter, soil, and belowground legacies. Ground-based harvesting and yarding systems can cause soil disturbances and compaction. The intensity of such disturbances will depend on the moisture content of the soil, size of material to be removed, equipment characteristics, number of passes of the equipment over the same area, depth of litter, soil type, and slope. The effects of timber harvest on legacies in soil and litter have been described elsewhere (Isaac, Hopkins, and Howard 1937; Graecen and Sands 1980; Wert and Thomas 1981; Geppert, Lorenz, and Larson 1985; Perry et al. 1989; Poff 1996; Pilz and Perry 1984; Perry and Amaranthus 1997; Hagerman et al. 1999; Neary, DeBano, and Ffolliott 2000; Byrd et al. 2000; Beschta et al. 2004; Karr et al. 2004; Sections 7.3 and 7.6). These effects do not always result in significant disturbances because they may be prevented through the use of aerial yarding and other low impact methods.

Where forestry practices include slash burning, there will also be effects on legacies in soils. The prolonged soil heating produced by smoldering combustion has been found to kill soil-stored seed and soil organisms, and to consume soil organic matter that supports soil biota. A wide variety of literature also addresses how soil legacies may be affected by slash or other surface fuel burns (Isaac, Hopkins, and Howard 1937; Pilz and Perry 1984; Frandsen and Ryan 1986; Albin et al. 1996; Poff 1996; Neary et al. 1999; Neary, DeBano, and Ffolliott 2000; Odion and Davis 2000; Brown, Reinhardt, and Kramer 2003; Korb, Johnson, and Covington 2004; Sections 7.3 and 7.6). Effects will vary considerably depending on fuel load, moisture, particle sizes, and whether broadcast or pile burning methods are used. Disturbances from forestry roads are another consideration. Roads increase the frequency and regularity of sediment inputs into streams (Section 6), and can lead to landslides (Jones et al. 2000, reviewed by Forman et al. 2003). Road-related disturbances vary considerably depending on characteristics of roads and the environment in which they are placed (Forman et al. 2003).

In sum, technology and techniques for harvesting and transporting trees, and treating harvested sites, vary and have changed over time. There are many options, leading to a wide range in net disturbance

intensity. There are also effects that are particular to certain life history groups (Sections 6 and 7), geography, and site-specific circumstances. These and other factors need to be considered when evaluating the intensity of forestry disturbances, making a case-by-case approach necessary.

4.0 A CONCEPTUAL MODEL FOR EVALUATING DISTURBANCE EFFECTS ON BIODIVERSITY

When the primary controls on local and regional species diversity are considered in concert, biodiversity may be best protected where intermediate disturbance regime effects prevent uniformly stressful circumstances and/or dominance leading to competitive exclusion, habitat heterogeneity, and retention of functional legacies (Figure 4.1). The conceptual model shown in Figure 4.1 can be used to evaluate disturbance effects, and further how they may be manipulated to influence biodiversity. Note that the importance of both additional habitat heterogeneity and biological legacy retention is assumed to decrease with increasing levels of these (i.e., the relationship is assumed to be asymptotic). This is a key information gap that research needs to address (Section 14.1).

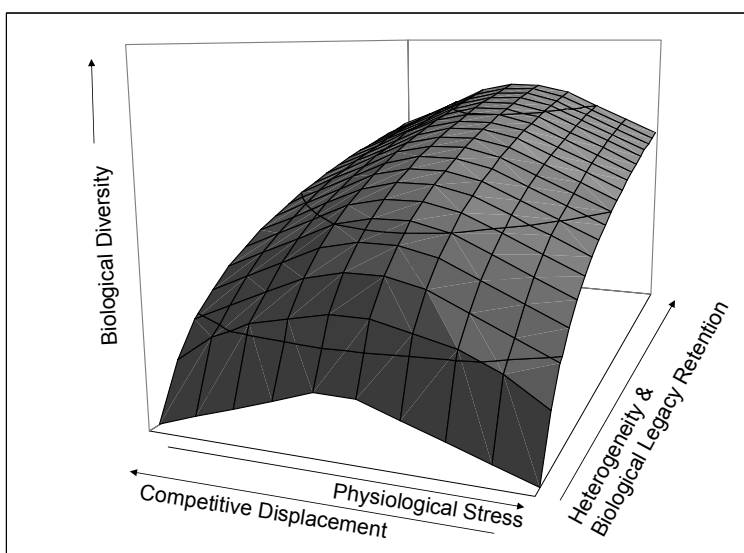


Figure 4.1 Conceptual Model for Evaluating How Forestry Disturbance May Influence Biodiversity (based on species diversity concepts)

The x-axis in Figure 4.1 is complicated because the effect of disturbance on resource availability or physiological stress depends upon the sensitivity of the taxon group of interest as well as geographic setting. However, it is possible to make predictions of biodiversity responses to disturbance in different settings (Section 4.2), but it is vital to first understand aspects of geographic variation in abiotic and biotic factors.

4.1 Linking Effects of Geographic Variation

Across large spatial extents, variation in climate causes not only regionalization in vegetation composition and structure, but also gradients in moisture, temperature, canopy architecture, woody debris recruitment, and understory light. Climate also manifests sharp contrasts in riparian forest productivity across the study area, with corresponding effects on species diversity. From west to east, local woody plant richness shows unimodal relationship with site productivity, with low values in both the highly productive Oregon Coast Range, where biotic control is greatest, and in the least productive eastern Cascades shrub-steppe where abiotic control is strongest (Waring et al. 2002). Highest local woody plant richness occurs in the somewhat intermediate southern Cascades and Siskiyou Mountains, where both controls are moderate (Ohmann and Spies 1998; Waring et al. 2002) (Figure 4.2). Local scale studies in western Oregon support the hypothesis that competition is a strong control on local plant richness in productive forests. For example, old-growth forests with active gap processes, silviculturally thinned stands, and early seral communities all harbor higher plant species richness than dense, even-aged conifer stands (Schoonmaker and McKee 1988; Stewart 1988; Bailey et al. 1998), especially fertilized plantations (Thomas et al. 1999).

The potential for positive effects of natural disturbances (and possibly silvicultural treatments) on richness will be greatest in productive riparian forests, such as occur in western Cascades and Coast Ranges of the Pacific Northwest, where competitive pressures are believed to be strongly governing local plant diversity (Pabst and Spies 1998, 1999; Hibbs and Bower 2001; Waring et al. 2002). In relatively unproductive forests of the eastern Cascades or Siskiyou, in contrast, a similar disturbance might add to physiological stress and lead to lower local diversity. There, plant diversity is locally high in undisturbed forests where local drought or infertility limits overstory density (Whittaker 1960; Stewart 1988).

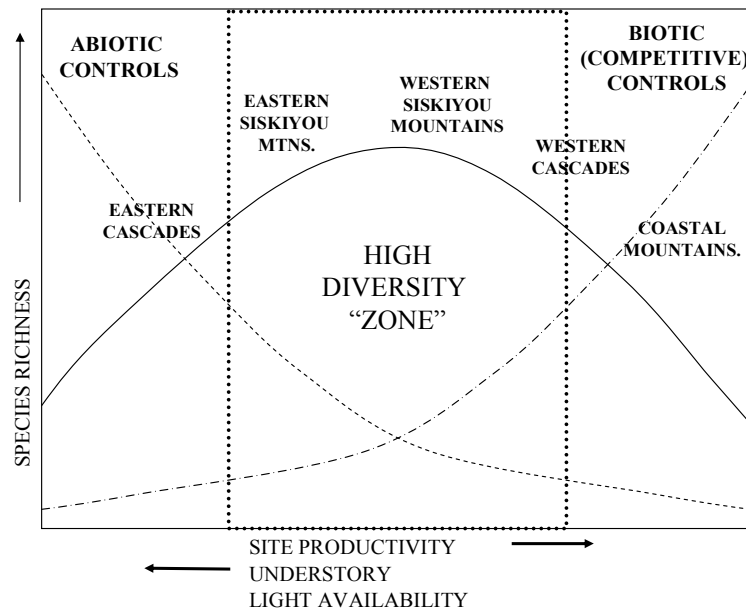


Figure 4.2 Conceptual Relationship between Local Riparian Vascular Plant Species Richness (solid line) and Site Productivity at Riparian Forest Sites across the Study Region (Dashed line shows abiotic controls, dot-dashed line shows biotic controls.)

From these general climatic patterns and empirical relationships among climate, productivity and forest structure (Appendix A), and the importance of biotic and abiotic processes (Figure 4.2), we constructed Figure 4.3, which illustrates the hypothesized relative importance of habitat heterogeneity, legacy retention, resource availability, and physiological stress across the climatic gradient.

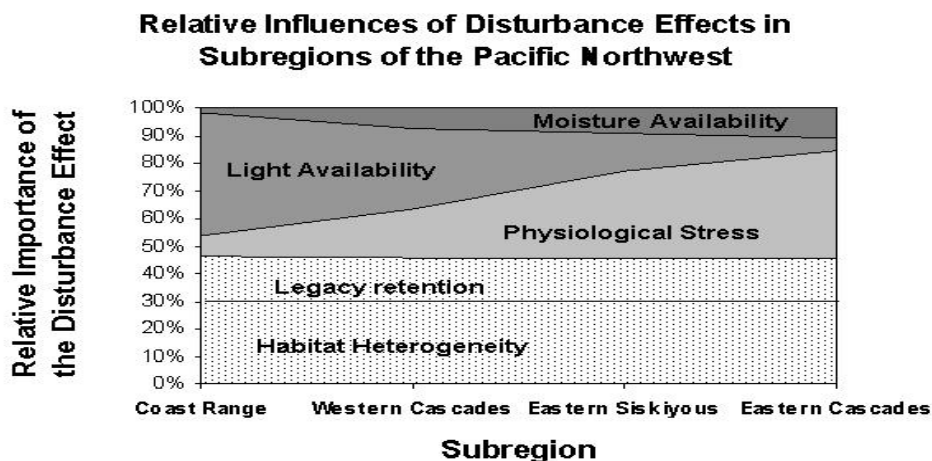


Figure 4.3 Relative Importance of Disturbance Effects on Factors Affecting Species Diversity in Sub-Regions of the Pacific Northwest

4.2 Evaluating the Effect of Riparian Forest Management on Biodiversity across the Pacific Northwest

In preceding sections, we developed a model for evaluating disturbance/biodiversity relationships using basic ecological principles. Here we describe how to make predictions about forestry disturbances in riparian zones using this model. Geographic variation in disturbance-associated stress and resource availability must also be accounted for. To illustrate this, we evaluate the model here for two relative geographic extremes in the region. These extremes are the wet temperate riparian forests west of the Cascades, and the xeric, interior riparian forests on the east slope of the Cascades and extreme easternmost Siskiyou Mountains. As a starting point, we will assume that forests in both areas are 30-60 years old, conifer-dominated, and regenerated post-harvest. There are many other scenarios, but these are likely to be relatively common in riparian forests of private timberland.

It is important to emphasize that life history traits (Sections 6 and 7) will cause variation in how different taxonomic groups respond to disturbance, particularly in terms of physiological stress. We discuss this further in Section 9.0. Nonetheless, this comparison should illustrate how different forestry disturbances affect biodiversity maintenance in varied geographic settings.

In Table 4.1, we evaluate several forest management options and rank their potential to maintain biodiversity based on our conceptual model. The management approaches comprise a gradient in intensity from no touch buffers to even-aged, short rotation clearcutting. It is assumed in no touch buffers that managers will prevent natural disturbances like fire and insect epidemics to the maximum extent possible. In the numerical rankings in the table, heterogeneity both at local and larger scales

contributes to biodiversity maintenance. Therefore, heterogeneity is more heavily weighted. Relative potential for biodiversity maintenance increases with numerical value calculated as the row sum in the table with low=1, medium=2, and high=3 for heterogeneity and legacy columns, and low and high =1 and medium =3 for resource availability and physiological stress. Values ranging from 1-2 or 2-3 were given the average (i.e., low-medium = 1.5 for legacy retention).

Table 4.1 Effects of Different Forest Management Options on the Fundamental Drivers of Biodiversity and Their Relative Potential for Maintaining Biodiversity in 30-60-Year-Old, Second Growth Riparian Forest Landscapes on the Wet Temperate West Side (W) and Xeric East side (E) of the Cascades

MANAGEMENT APPROACH	RANKING CRITERIA					Potential for Biodiversity Maintenance
	Local Heterogeneity	Landscape Heterogeneity	Legacy Retention	Resource Availability	Physiological Stress	Sum
Protection from disturbance (no touch buffer)	W&E-Low	W-Low E-Low-Medium	W&E-High	W- Low E -Low-Medium	W&E-Low	W=7 E=8.5
Uneven-aged Single tree selection	W-Low-Medium E- Medium	W-Low E-Low-Medium	W&E-Medium-High	W-Low-Medium E-Low-Medium	W-Low E-Low-Medium	W=7 E=10
Uneven-aged Thinning from below	W&E-Medium-High	W&E-Low	W&E-Medium-High	W-Low E-Medium	W-Low-Medium E-Medium	W=9 E=12
Uneven-aged Small patch selection	W&E-Medium	W&E-High	W&E-Medium	W&E-Medium	W-Low-Medium E-Medium-High	W=12 E=12
Even-aged shelterwood	W&E-Medium	W&E-Medium	W&E-Low-Medium	W&E-High	W-Medium-High E-High	W=8.5 E=7.5
Even-aged clearcut (80-120 years)	W&E-Low	W&E-Medium	W&E-Low	W&E-High	W-Medium-High E-High	W=7 E=6
Even-aged clearcut (40-60 years)	W&E-Low	W&E-Low to Medium	W&E-Low	W&E-High	W-Medium to High E-High	W=6.5 E=5.5

Based on the rankings in Table 4.1, a productive westside riparian forest with little or no disturbance (single tree selection or no touch buffer) and a forest subjected to short-rotation clearcutting would harbor the lowest potential for biodiversity maintenance. In the former case, this would be expected because of low heterogeneity and resource availability resulting from strong dominance by the young conifers. With short-rotation clearcutting, low heterogeneity, low legacy retention, and possibly high physiological stress would be the limiting factors. Small patch harvesting, followed by thinning from below, and even-aged shelterwood are the forest management actions that ranked best in terms of maintaining biodiversity in the westside example. These management options would likely allow maintenance of biodiversity by adding heterogeneity and increasing resource availability, while maintaining biological legacies. In the exceptionally mild environments of the coastal mountains, where sites quickly reforest following disturbance, relatively severe disturbances (shelterwood) may be consistent with the maintenance of biodiversity, so long as they are not too frequent and retain sufficient legacy features and heterogeneity remain to provide refugia for sensitive taxa.

In the eastside environment, small patch selection and thinning from below ranked best for biodiversity maintenance. Several important differences are likely to be associated with forest management in eastside vs. westside riparian forests. First, greater ambient fluctuations in temperature and insolation increase the importance of the forest for moderating temperature extremes on the eastside. Second, the forests are less likely to develop as densely and understory light may be relatively less limiting than on the westside (Grier and Running 1977). In addition, other forms of heterogeneity (e.g., topographic moisture gradients with upslope areas) are increasingly important for differentiating habitats in eastside forests (Appendix A). Consequently, undisturbed stands may be less uniformly dominated by the overstory conifers and less dependent upon disturbance for maintenance of biodiversity. At the same time, the negative effects of moderate and severe disturbances on microclimate are more likely, so even-aged systems (shelterwood, clearcutting) would likely create stressful environments and lead to other stresses on biodiversity, such as stream heating. As in westside forests, the intermediate intensity management techniques blending legacy retention, moderate microclimatic stress and resource availability, and moderate to high local and landscape heterogeneity appear likely to be most appropriate for biodiversity maintenance. Thus, despite geographic differences, a number of intermediate intensity forest management approaches may be consistent with the maintenance of biodiversity, as predicted in Section 3.2.

The principles articulated here should provide a consistent conceptual basis to evaluate both natural and human disturbances. Up to this point we have kept the discussion intentionally general, discussing biodiversity in its broadest sense. Some groups may thrive on the resources liberated by disturbance, whereas others are more closely linked to the protected environment of established riparian forests. It is likely that managers will have interest in the evaluation of forest management effects on specific taxonomic groups, such as those that are imperiled (spotted owls, murrelets), or have great economic or societal interest (salmon). For such analyses, a much more detailed understanding of life history characteristics is desirable. In Sections 6 and 7, we summarize effects of riparian forest management on several different taxa groups to illustrate the important interactions between management and species' life history.

5.0 POLICIES FOR PROTECTING RIPARIAN AREAS

Prior to 1970, there were no streamside protection policies related to timber harvest. Since 1970, numerous state and federal regulations have been developed and modified, and future modification appears likely. The complex, context-dependent regulations are not detailed here. Recent reviews are available: Gregory (1997) and Young (2000).

Riparian management policies that have been developed in the last decade or so focus on a) widths of riparian management zones, b) retention of living and dead trees within the riparian zone, c) extent of shade, d) floodplain protection, e) yarding corridors, f) culvert dimensions, g) road crossings, h) felling techniques, and i) erosion protection (Gregory 1997). The riparian management zone may be much narrower than the riparian area based on a functional definition of that area, and the criteria used in the definition (Gregory 1997).

Regulations for private landowners differ considerably among the states of Alaska, Washington, Oregon, and California. Standards are further modified within the states based on regional conditions. All jurisdictions protect all but ephemeral streams using riparian management zones, but the zones differ in size and what is allowed within them. The state of Oregon has a policy of protecting streambanks with a no-harvest zone extending 3.5 m from the edge of the stream. Alaska allows no harvest within 30 m of unconstrained anadromous fish bearing streams. Criteria for what must be retained after harvest differ. It should be noted that while riparian management zone guidelines do not necessarily severely restrict activities in riparian areas, these guidelines might often be subordinated where there are water quality issues or species protected under state or federal law.

Riparian guidelines lack an explicit vision of desired future conditions or dynamics. Such a vision would be highly context-dependent. Young (2000) notes that because existing guidelines allow the harvest of large conifers, typical harvest rotations of 60-80 years under existing guidelines can eliminate natural riparian sources of *large* woody debris resources from streams. This illustrates how resource availability in many cases may be under the discretion of the landowner. In many state and private lands, past harvest has already eliminated the larger sources of woody debris. Near-term approaches to increasing large woody debris, regulatory or not, could involve bringing it in from outside the riparian area. Riparian management guidelines in Oregon include an active management option that uses a basal area credit system, which allows for increased volume of harvest where logs are placed in streams and for other resource enhancements.

Gregory (1997) notes that the basis for selection of specific numerical criteria may have been the result of a negotiated consensus, and the specific reasons for numerical criteria may be poorly documented. Whether these or more explicit rule-based approaches are more effective in terms of protection goals is unclear. However, the diversity of riparian practices that have occurred, including those on federal lands, should prove to be an asset in advancing our understanding of what are the most effective approaches where resource protection is a goal.

PART II: TAXA SPECIFIC INFORMATION

Researchers from Oregon State University and the U.S. Geologic Survey who are knowledgeable with the taxonomic groups provide separate chapters here. These treatments are summaries of existing information, not extensive treatments, but sources of further information are provided. There is no treatment of mollusks. Mollusks have very narrow ranges and specific habitat requirements, and warrant attention, but there are relatively few experts on these organisms in the Pacific Northwest.

Each of the authors below describes life history attributes, habitat requirements, and ecological processes in relation to forestry practices. The authors also provide guidelines for management that can help sustain the particular taxonomic group, as well as a section on research needs. More general research needs are discussed in Section 14. There are, however, differences between these chapters based on specific attributes of the group of organisms.

6.0 FORESTRY PRACTICES AND AQUATIC BIODIVERSITY

6.1 Fish

Robert E. Gresswell
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center
3200 SW Jefferson Way
Corvallis, Oregon 97331.

6.1.1 Introduction

In the Pacific Northwest, fish communities are found in a diverse array of aquatic habitats ranging from the large coastal rivers of the temperate rainforests, to the fragmented and sometimes ephemeral streams of the xeric interior basins, and high-elevation streams and lakes in the mountainous areas (Rieman et al. 2003). Only high-elevation lakes and streams isolated above barriers to fish passage remained historically devoid of fish because they were never invaded following Pleistocene glaciation (Smith 1981). Despite this widespread distribution and once great population abundances, taxonomic diversity of fishes in these forested systems is naturally lower than in aquatic habitats in the eastern U.S. (Reeves, Bisson, and Dambacher 1998).

Interactions among factors that influence species richness in aquatic systems (e.g., basin size, long-term stability of habitat, and barriers to colonization; Smith 1981) continue to influence the occurrence and persistence of fishes in these systems today. Consequently, the larger low-elevation rivers and estuaries support the greatest variety of fish species. In the high-elevation tributary streams, fish communities are less complex because these aquatic systems were less climatically and geologically stable, and fish populations were smaller and more prone to local extirpation. Furthermore, barriers to fish passage inhibited dispersal and colonization (Smith 1981). Streams in forested landscapes generally support salmon and trout, *Oncorhynchus* spp., whitefish *Prosopium* spp., sculpins *Cottus* spp., suckers *Catostomus* spp., and minnows (Cyprinidae), but in some of the colder streams, charrs (e.g., *Salvelinus confluentus* and *Salvelinus malma*) and lampreys (Petromyzontidae) may also occur (Rieman et al. 2003).

Although biodiversity defined in terms of fish species richness is low in the Pacific Northwest, intraspecific variability is high, and polytypic fish species are common in the diverse aquatic habitats of the region. For example, the salmonids in the coastal rivers and streams, and the larger interconnected streams, rivers, and lakes of the interior exhibit a variety of ecotypes and migratory life histories (Healey 1986; Trotter 1989; Larson and McIntire 1993; Northcote 1997). This life-history variation appears to be associated with adaptation to spatial and temporal variation in environment (e.g., Schaffer and Elson 1975; Carl and Healey 1984; Beacham and Murray 1987), and there is some evidence of the genetic heritability of life-history traits (Carl and Healey 1984; Gharrett and Smoker 1993; Hankin, Nicholas, and Downey 1993). Persistence of any level of biological organization (e.g., life-history type, population, metapopulation, subspecies, species, community) is related to the interaction of environmental and biological components, and intraspecific diversity is a means of spreading risk (*sensu* den Boer 1968) of extirpation in dynamic environments (Gresswell 1999).

Unfortunately, despite the broad distribution and extensive intraspecific diversity, persistence of native fishes is uncertain in the Pacific Northwest. Many populations of anadromous salmonids, once synonymous with vigorous biological communities throughout the region, are threatened with extinction (Nehlsen, Williams, and Lichatowich 1991; Frissell 1993; Thurow, Lee, and Rieman 1997). Furthermore, over half of the native taxa in the Columbia River Basin are either listed under the Endangered Species Act, are being considered for listing, or are deemed sensitive by the

management agencies (Lee et al. 1997; Thurow, Lee, and Rieman 1997). Potamodromous species like bull trout *Salvelinus confluentus* are estimated to occur as strong populations in less than 5% of their potential range (Rieman, Lee, and Thurow 1997). Although not currently listed under the endangered species list, the coastal cutthroat trout *Oncorhynchus clarki* is managed as a sensitive species in Oregon and California (Hall, Bisson, and Gresswell 1997). Native non-game fishes have rarely been monitored, but populations of species such as large-scale suckers (*Catostomus macrocheilus*), squawfish (*Ptychocheilus umpqua*), and Pacific lamprey (*Lampetra tridentata*) also are declining in some drainages (Oregon Department of Fish and Wildlife, unpublished data).

6.1.2 Ecological Processes and Habitat Features Related to Forestry Practices

Compared to other land uses (e.g., agriculture or urban development), forestry is typically associated with greater aquatic diversity (Potter et al. 2004) and fish abundance (Pess et al. 2002). Nevertheless, historic timber harvesting and associated road construction practices that did not consider stream protection needs are linked to declines in diversity and abundance of salmonid species in the Pacific Northwest (Bisson et al. 1987, 1992; Nehlsen, Williams, and Lichatowich 1991; Sedell and Beschta 1991; Reeves, Everest, and Sedell 1993). Effects of timber harvest on aquatic systems may be both direct and immediate (i.e., pulsed disturbance; Yount and Niemi 1990) or indirect and sustained over an extended period (i.e., press disturbance; Yount and Niemi 1990). Timber harvest can affect stream ecosystems by altering hydrological patterns, stream temperature and solar insolation, habitat complexity, organic debris delivery and accumulation, sedimentation, and channel morphology (Hall and Lantz 1969; Brown and Krygier 1970; Everest et al. 1987; Gregory et al. 1987; Bilby and Ward 1991; Chamberlin, Harr, and Everest 1991; Johnson and Jones 2000). The magnitude and scale of effects are related to the size and intensity of the harvest, yarding techniques, geology, topography, watershed size, and amount, magnitude, and timing of post-harvest precipitation events (Murphy and Hall 1981; Swanson et al. 1989; Hicks et al. 1991). Furthermore, Best Management Practices, such as changes in logging systems, reforestation techniques, and riparian management areas, can moderate both generation and delivery of materials and energy to streams (Bisson et al. 1992; Ice 2004).

Reeves, Everest, and Sedell (1993) surveyed 14 watersheds (200-5,200 hectares) between 1985 and 1988 that had from 0-100% of the basin harvested. They used a two-sample t-test to compare density of juvenile anadromous salmonids between the two groups of watersheds (<25% and >25% harvested). There was no reference to when harvest occurred prior to 1985. They determined that diversity of juvenile salmonid assemblages was directly related to the proportion of the watershed that had been harvested, and diversity decreased when >25% of the basin had been harvested. Furthermore, basins that experienced a high level of harvest were more frequently dominated by a single salmonid species. Instream habitat heterogeneity was also directly related to level of harvest, and streams in low-harvest basins had significantly more pieces of wood per 100 m and more pools per 100 m than streams in high-harvest basins (Reeves, Everest, and Sedell 1993). Similar results have been documented for streams in Washington (Bisson and Sedell 1984) and coastal Oregon (Hicks et al. 1991).

Examining the extent of harvest provides important context for these findings. In the 23 years between 1972 and 1995, almost 20% of 4.6 million forested hectares in three provinces of western Oregon were subjected to clear-cut harvest, and the greatest concentration of cutting occurred on private industrial lands in the moist Coast Range Province (Cohen et al. 2002). When compared to public and non-industrial private landowners, private industrial landowners also had larger individual cutting units that were more spatially aggregated through time (Cohen et al. 2002). These data suggest that lands managed by private industrial landowners would have lower salmonid diversity and a higher probability of supporting only a single salmonid species.

The amount of time between natural disturbance events varies within and among basins (Poff and Ward 1990), and the temporal aspect of disturbance is an important part of the habitat template that likely influenced evolution of fishes inhabiting individual watersheds. Because natural recovery of stream systems may take decades to centuries (Gresswell 1999), substantially altering disturbance intervals by reducing times of harvest rotation may alter the system response and reduce persistence of fish in the system. Those systems that may exhibit the slowest recovery time following disturbance (e.g., eastside and higher elevation systems) would likely exhibit the largest negative response to repeated disturbances (Yount and Niemi 1990). Furthermore, it is important to recognize that response to a particular disturbance event is contingent on conditions remaining from previous events. Where natural recovery rates are unacceptably low, forest managers sometimes use active management practices in an attempt to restore key functions (Bisson et al. 1992; Ice 2000), but the results of these actions are often mixed (Kauffman et al. 1997).

Timber harvest potentially can affect water quality, water temperature, sedimentation, and channel structure (Chamberlin, Harr, and Everest 1991). For example, wood recruitment processes in small headwater streams are dominated by streamside landslides, toe slope-creep, and wind throw (May and Gresswell 2003a). A cycle of filling and spilling is common to many headwater streams in steep mountainous terrain. Over time, these channels fill with wood and sediment, which is episodically scoured by debris flows. Without a source of wood to increase the storage capacity of tributaries that have been scoured to bedrock following debris flow, these systems lose the capacity to store sediment and may persist in a bedrock state for an extended period (May and Gresswell 2003a).

The effects of vegetation removal on water temperature vary greatly among sites. Greater solar insolation following removal of riparian vegetation sometimes increases primary and secondary productivity in otherwise shaded streams (Murphy and Hall 1981; Murphy, Hawkins, and Anderson 1981; Hawkins, Murphy, and Anderson 1982; Hawkins et al. 1983), but lack of shade can also increase stream temperature and reduce salmonid habitat quality (Lantz 1971; Beschta et al. 1987; Johnson and Jones 2000). Where stream temperatures are not elevated excessively, however, instream productivity may increase (Gresswell 1999; Wilzbach 2005). There is also some evidence that even when water temperature increases are great at sites in headwater streams, changes may be negligible downstream (Gresswell 1999). Although water temperature of streams may increase after streamside vegetation is removed (Gray and Edington 1969), predicting the biological consequences is difficult (Beschta et al. 1987). Effects depend on the harvest intensity, size of harvest area, stream size, stream network complexity, watershed topography, normal temperature ranges of affected stream reaches, and life-history stage of the organisms present.

Effects of riparian vegetation diminish with increasing distance from the stream channel (Beschta et al. 1987; VanSickle and Gregory 1990; May and Gresswell 2003b). Estimates of the buffer width necessary to protect various riparian functions generally remain uncertain, but definitely vary according to individual function (e.g., root strength, large woody debris delivery to streams, large wood debris delivery to riparian areas, input of organic nutrients, shade, microclimate, water quality) (Castelle and Johnson 2000). In addition, site factors including geology, vegetation type, climate, topography, and watershed size influence riparian vegetation and its ecological role in an individual watershed.

Rieman et al. (2000) found a strong inverse relationship between stream biodiversity and road density throughout the Columbia River basin. Some negative effects of roads include persistent erosion of fine sediments, increased potential for slope failure, and passage barriers associated with stream crossing structures, especially culverts. In large-scale assessments, road density may indicate potential for declines in aquatic biodiversity, but these relationships are inextricably linked to historic practices and road locations. There is evidence that where problems can be identified with specific portions of a road, renovation can be very effective (NCASI 2003). For example, direct-delivery

culverts, where road sediment is discharged directly to the stream network, have been found to be an important and persistent source of fine sediment (Bilby, Sullivan, and Duncan 1989), but these locations can be corrected. In some watersheds where abundance of native fish populations has declined and passage barriers have isolated small headwater populations, vulnerability of fish populations to reductions in genetic diversity (Wofford, Gresswell, and Banks 2005), disturbance (natural and anthropogenic), and potential extirpation has increased (Medina and Martin 1988; Propst, Stefferud, and Turner 1992; Rinne 1996). Recognizing and correcting these passage barriers is critical for reconnecting the stream network and reducing this risk (Kauffman et al. 1997).

Watershed or larger scale considerations. Although many ecosystem components, and relationships among these components, are poorly understood in the Pacific Northwest, there is growing recognition that the answers to many of these ecological questions are scale-dependent (May 1974; White and Pickett 1985; Frissell et al. 1986). For instance, the spatial and temporal patterns of large woody debris inputs to streams are important because they influence channel morphology, routing and storage of water and sediment, and provide structure and complexity associated with habitat for numerous aquatic organisms. Streams exist in a dynamic environment where relatively frequent site-scale and episodic broad-scale disturbances play a major role in creating and maintaining aquatic habitat. These natural cycles of disturbance create a diverse array of habitat types and availability through time and space (Reeves et al. 1995).

Investigations concerning the effects of spatial scale on scientific understanding of the organization of aquatic species are becoming more abundant (e.g., Imhof, Fitzgibbon, and Annable 1996; Richards et al. 1997), and it is increasingly apparent that a multiscale approach may facilitate interpretation of spatially extensive data (Poff and Allen 1995; Caselle and Warner 1996; Wiley, Kohler, and Seelbach 1997). For instance, numerous studies have investigated, or are currently evaluating, the relationships between physical habitat and anadromous salmonids (Nickelson et al. 1992; Reeves et al. 1995). It is difficult, however, to develop strong inferences because anadromous fish spend at least part of their lives in the marine environment where they are affected by a much different array of environmental variables, including commercial harvest. In contrast, nonmigratory freshwater fishes (e.g., sculpins) and fishes that migrate only in freshwater (potamodromous fishes, such as some populations of coastal cutthroat trout) are dependent on adequate freshwater habitat throughout their lives. Freshwater fishes, therefore, may be more tightly linked to changes in aquatic habitats than anadromous species, but much less effort has been expended to describe these linkages. The relationship between land management and aquatic habitat may be especially relevant for the coastal cutthroat trout because land management activities are among the factors that may have contributed to their decline (Williams and Nehlsen 1997).

Regional Variation. At the regional spatial scale, Thurow, Lee, and Rieman (1997) investigated the current and historical distribution of seven native salmonids in the Upper Columbia River Basin (east of the Cascade Mountains) and attempted to expand the results of site-level information to broad landscape scales. Other studies have identified some factors influencing distribution and abundance for some potamodromous species, such as bull trout (*Salvelinus confluentus*) (Rieman and McIntyre 1995; Rieman, Lee, and Thurow 1997; Watson and Hillman 1997), but the relationships between habitat and freshwater aquatic organisms across broad spatial scales in western Oregon are poorly understood.

6.1.3 *General Guidelines for Sustainable Forestry Practices*

Available information suggests that managers need to recognize that maintaining habitat and population diversity is critical to the persistence of most aquatic species, and management activities that lead to environmental simplification and homogeneity may ultimately have substantial negative effects at several levels of biological organization. Although habitats have been degraded and numerous fish species have declined, the region, and forested landscapes in particular, still supports important elements of the historical diversity in native fishes. Large interconnected networks of stream habitats continue to exist in some aquatic systems of the Pacific Northwest, and listed species have migration corridors through large rivers and lakes, to and from the ocean. Furthermore, high quality habitats can be found in large roadless areas, and some depressed fish species (e.g., bull trout) still occupy the majority of their historical range (Rieman, Lee, and Thurow 1997; Thurow, Lee, and Rieman 1997; Williams and Nehlsen 1997). Given a continuation of historical management trends, increasing human density, increased pressure from invasive species, and extractive demands, the trend for some of these systems is not positive (e.g., Rieman, Lee, and Thurow 1997). Conservation of remnant strongholds, often associated with the forested watersheds, and restoration of natural processes critical for habitat formation, will both be necessary for organism persistence (Lee et al. 1997; Young 1995).

6.1.4 *Information Needs*

Determining the relative importance of interrelated factors underlying past declines and current trends in populations of wild anadromous fish is particularly difficult. Changes in ocean productivity and amounts of fish harvested have been superimposed on varying influences on freshwater habitat over several decades and increasing hatchery populations. The genetic integrity and overall fitness of many naturally functioning taxa are difficult to predict without a better understanding of how freshwater habitat is functioning at landscape and regional scales. For example, much of the information available concerning factors that regulate woody debris input is limited to smaller spatial areas; little is known about woody debris recruitment, retention, and distribution at broader scales. Increasing our understanding of the physical and biological factors that influence these processes, and how these processes interact to influence fish populations, is crucial for the development of land management strategies that are compatible with persistence of native organisms.

Very little is known about fishes in the headwater portions of stream networks, and these small channels are often directly impacted by land use activities. Previous policies and management activities often failed to recognize the value of small channels and their associated riparian habitats (Beschta and Platts 1986). Indeed, small headwater stream channels can represent greater than 70% of the cumulative channel length in mountain watersheds (Benda et al. 1992). These headwater channels are important conduits for water, sediment, and wood routed from hillslopes to larger streams (Naiman et al. 1992; May and Gresswell 2003a).

Interactive effects of current logging practices on public lands administered by federal and state agencies and private timber lands that are managed primarily for commodity production are poorly understood. Determining the effects of land management activities on aquatic habitat, and ultimately aquatic organisms, is hampered by the complexity of interrelationships among physical, chemical, and biological characteristics of terrestrial, riparian, and aquatic systems, especially at broader spatial scales. The difficulty in developing a reliable long-term record of land use, land cover information, and additional stressors of species being studied also hampers progress. Frissell et al. (1986) developed a method for classifying stream systems in the context of the watersheds of which they are a part, and this approach is becoming more broadly accepted as a means of expanding understanding of the influence of disturbance and land management at the watershed scale (Imhof, Fitzgibbon, and Annable 1986). Despite a call for an increased emphasis on broader scale, integrated research, most

studies are still conducted at the habitat-unit scale, and protocols for examining these data in a broader context have not been adequately developed (Imhof, Fitzgibbon, and Annable 1986; Poole, Frissell, and Ralph 1997; Smith, Gresswell, and Hayes 1997).

6.2 Stream Amphibians

R. Bruce Bury
U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center
3200 SW Jefferson Way
Corvallis, Oregon 97331

6.2.1 Introduction

Stream amphibians of the Pacific Northwest often are the dominant vertebrates in headwaters and small streams in terms of numbers of individuals and biomass (Bury et al. 1991). Larvae mostly eat aquatic invertebrates with a shift toward larger prey items with growth. Adults of giant salamanders eat large-sized invertebrates, other amphibians, and even small mammals (Bury 1972).

Three endemic families of stream amphibians occur in the Pacific Northwest, and all breed and deposit their eggs in flowing water (Nussbaum, Brodie, and Storm 1983; Bury 1994): torrent salamanders (4-5 species), Pacific giant salamanders (4 species), and tailed frogs (2 species). They apparently require rocky, flowing streams with closed forest canopies where temperatures remain cool year round, and they are most abundant in late seral stages of forests (Welsh 1990; Adams and Bury 2002; Welsh and Lind 2002). There is concern about the conservation status of the Southern torrent salamander because it was earlier petitioned for Federal listing, but was found not warranted at that time. The Southern torrent salamander is the most sensitive of the stream amphibians to timber harvest impacts (Corn and Bury 1989; Welsh and Lind 1991), closely followed by the tailed frog.

The torrent salamanders are small-sized, stocky salamanders that frequent seeps, headwaters and cascading, small streams. Juveniles and adults rarely venture farther than 1 m from water. Welsh and Lind (1996) reported that the Southern torrent salamander occurs in a narrow range of conditions: cold, clear headwaters to low-order streams with loose, coarse substrates (little sedimentation), in humid forest habitats with large conifers, abundant moss, and >80% canopy closure.

Tailed frogs occur from headwaters to third order streams (generally <2 m wide) but on occasion are found in larger waters, perhaps being swept downstream in seasonal flooding. Tailed frogs are adapted to fast, rocky streams: larvae have a streamlined body, muscular tail, and a large suctorial mouth to attach to rocks. The eggs of this primitive amphibian are slow to develop, averaging 6 weeks to hatching (Brown 1989). Most larvae metamorphose after 2 years in the Coast Ranges and 3-4 years in inland or northern sites (Daugherty and Sheldon 1982; Bull and Carter 1996; Brown 1990; Wahbe 1996). They transform in only 1 year in coastal parts of southern Oregon and northern California (Wallace and Diller 1998; Bury and Adams 1999).

Both torrent salamander and tailed frogs appear to be negatively impacted by elevated stream temperatures and siltation resulting from clearcut timber harvest (Bury and Corn 1988a; Corn and Bury 1989; Dupuis and Steventon 1999; Biek, Mills, and Bury 2002; Welsh and Lind 2002). They are absent in open or dry slopes such as oak woodland. Pacific giant salamanders range from headwaters to large streams, sometimes in waters with partial canopy. Most egg deposition sites are in subterranean habitats (e.g., underground seeps). The larval stage is about 17-18 months long. Larvae and adults may grow to 1 ft long (300 mm). Adults sometimes occur in upland forests during rainy periods. They co-occur with native salmonid fishes in some larger waters. Although their numbers may be depleted by logging in some areas, the giant salamander appears to persist in watersheds that receive timber harvest.

In the Pacific Northwest, there are also several plethodontid (lungless) salamanders in or near streams. The Van Dyke's Salamander (*Plethodon vandykei*), frequents seeps and rocky talus in forested stands. They seem to prefer streams within older forests, but there are no trend data available on populations. Similarly, Dunn's Salamander (*Plethodon dunni*) occurs in wet rock rubble or talus, most often along creeks and streams.

Larger streams have slow pools and side waters that are used by several other species of amphibians, mostly for breeding. Stream order 3 and larger waters may have yellow-legged frogs (*Rana boylei*), a stream specialist. These frogs live along the edges of the waters, often jumping from shore or land into the stream when disturbed.

6.2.2 Ecological Processes and Habitat Features Related to Forestry Practices

The number of species, densities and biomass of stream amphibians are significantly greater (2–10X) in streams flowing in natural than in logged forests (Corn and Bury 1989). Tailed frogs are reduced by timber harvest where logging opens up large tracts in watersheds or leaves no buffer areas (Bury and Corn 1988b; Corn and Bury 1989; Welsh 1990; Bury et al. 1991; Bull and Carter 1996; Dupuis and Steventon 1999).

Immediate changes occur in stream habitats due to loss of streambank vegetation or from upslope activities (e.g., road development, timber harvest). Logging practices often result in sedimentation, which degrades amphibian habitat by reducing access to cover sites (Corn and Bury 1989; Dupuis and Steventon 1999). Steeper gradients tend to flush out sediments, which may mitigate silt inputs from logging (Hall, Murphy, and Aho 1978). Large downed wood in streams also provides energy input to the stream ecosystem and adds stability to the stream flow. Natural recruitment of such material is lost with removal of large trees. Replacing and maintaining woody debris in streams where natural recruitment is lost or reduced is a simple step that will help maintain aquatic biodiversity regardless of stand objectives.

The nature of the bedrock or parent geology is important in determining the severity of sedimentation. In managed stands in western Washington, Wilkins and Peterson (2000) found greater abundance of all stream species as gradient increased. Further, they reported fewer giant salamanders and absence of tailed frogs in drainages underlain by sediment of marine origin compared to those underlain by basalt (more fragmented rock present). In contrast, stream amphibians were found in many drainages with marine sediments inside Olympic National Park, a large forested reserve (Adams and Bury 2002). This suggested that timber harvest has a more severe effect on amphibians in areas underlain by marine sediments.

Forest harvest, especially clearcutting, increases insolation and raises stream temperatures, thereby increasing microbial respiration, primary production, invertebrate consumers, and populations of predators on amphibians. Tailed frogs are the least tolerant of any frog to elevated temperature, and die quickly when exposed to water temperatures near 29.6°C (deVlaming and Bury 1970). Exposure to temperatures at 24°C for several hours may be lethal (Metter 1966; Claussen 1973). Further, their eggs perish at >18.5°C (Brown 1975). This may be their “weak link” because tailed frogs nest in summer when water temperatures are at their peak. Similarly, torrent salamanders require cool temperatures (Bury and Nebeker, pers. obs.; Pilliod et al. 2003): larvae die at 26.7°C (range 25.6–27.4°C) and adults at 27.9°C (range 26.3–29.3°C). These are the lowest values known for any stream amphibian. Thus, timber harvest or other factors that elevate stream temperatures to approach or exceed these values are of concern to the maintenance of “healthy” conditions for headwater amphibians in the Pacific Northwest.

There are no studies that directly relate size of forest harvest areas to stream conditions for stream amphibians. Corn and Bury (1989) found that tailed frogs and torrent salamanders sometimes

occurred in logged areas if there was uncut mature forest upstream. In contrast, these species were lacking in some uncut forest if some logging had occurred above the area. These spatial relationships need further study.

Stream amphibians occur in managed stands (Diller and Wallace 1996; Olson et al. 2000a, 2000b, 2000c; Wilkins and Peterson 2000), but often at reduced numbers except in maritime influenced areas, where summer fogs ameliorate summer temperatures. We know little about how frequency of harvest regimes (rotation age) affects stream amphibians. However, we recently found that stream amphibians in the Oregon Coast Range had not recovered 35-50 years after clearcut harvesting (Bury and Pearl 1999; B. Bury and D. Major, in prep.). Harvest of stands every 60-70 years may be too frequent for populations of sensitive species (torrent salamander and tailed frog) to recover.

In northern California, some recent forest practice rules have improved riparian protection over the past. Streams now have equipment exclusion zones and tree retention from 15-30 m on each side of streams (Diller and Wallace 1996). However, Welsh and Lind (1996) reported that there is still a serious problem with the misclassification of streams where the faulty assumption is made that aquatic life does not exist in particular channels; this results in inadequate protection. Further, the protection width is very narrow (15 m) and may not maintain required microclimatic conditions for the torrent salamander. And, the canopy can be reduced to 50% of pre-harvest levels after each entry.

Effective width of buffer areas is unclear. Maximum shading capacity may be within a width of 25 m, and 90% of that capacity occurs at 17 m (see Budd et al. 1987). However, widths of 30 m or more are needed to stabilize microclimates within streamside riparian zones (Brosofske et al. 1997). To reduce sediment flow and maintain other riparian functions, the minimum buffer width may need to be 60-80 m wide (Ledwith 1996; Welsh et al. 1998) or up to 100 m (McComb, McGarigal, and Anthony 1993). Recently, Vesely and McComb (2002) reported that minimum buffer strips on most private forests (6.1 m along medium-sized streams and no buffers along headwaters in Oregon) may not be sufficient to ensure that amphibian communities in managed stand remain as diverse as in unlogged forests. They recommended extension of riparian buffer strips to permanent headwater streams and buffer strips 20 m wide or more on all streams.

Watershed or larger scale considerations. Although adults of the tailed frog are considered to be closely associated with streams (Blaustein et al. 1995), they occur in forests 100-500+ m from water during the wet season (Corn and Bury 1991; Wahbe, Bunnell, and Bury 1999). Also, Bury and Corn (1987, 1988b) captured many recently metamorphosed *Ascaphus* in pitfall traps set in forested stands near streams. These data suggested recently metamorphosed animals disperse into surrounding forests by autumn. Thus, retention of shade from riparian zones and adjacent forests may be critical to the survival and dispersal of even those stream amphibians with high fidelity to the stream channel.

Tailed frog populations show strong genetic differences among watersheds (Ritland et al. 2000), suggesting low movement potential. Similarly, genetics of torrent salamander in most watersheds of are highly distinctive (Good and Wake 1992). In fact, the four species currently recognized are as genetically distinct as most families of birds and mammals, reflecting the ancient lineage and isolation of torrent salamanders.

Regional Variation. In northern California, Diller and Wallace (1996) found that torrent salamanders appeared to occur in managed stands more frequently in maritime areas than at interior locales. These findings are consistent with a hypothesis that the local effects of harvest depend upon the magnitude of temperature changes with canopy removal, which increase from the coast inland. Similar findings may also conceivably apply along latitudinal gradients.

6.2.3 General Guidelines for Sustainable Forestry Practices

Diller and Wallace (1996) report that recent forestry practices are improvements over the past, including tree retention standards for 15-30 m on each side of streams, better road construction, and logging practices (e.g., cable logging). A two-tiered approach (deMaynadier and Hunter 1995; Vesely and McComb 2002) suggests protection of a narrow (e.g., 10-25 m, each side) no-cutting zone adjacent to the stream corridor, surrounded by a wide zone where limited harvesting may take place (e.g., removal of 25% of the basal area).

We may profit from suggestions of Budd et al. (1987) who stated “Width of the riparian zone varies from stream to stream and along the course of an individual stream. In the Pacific Northwest, stream buffer widths for each side range from 11 m to 38 m, depending on the riparian ecosystem element studied.” Further, deMaynadier and Hunter (1995) recommended adjusting buffer width proportionally to a) stream width, b) the intensity of adjacent harvest, and c) slope. We may need to invoke “adaptive management” (learn as we go) or “adaptive protection” where we employ a variable buffer width that reflects a suite of local (e.g., type of harvest, stream gradient) and regional factors (climate, soils).

6.2.4 Information Needs

Our collective goals may be better served by reducing reliance on a set of physical criteria such as buffer widths at 30 m and paying more attention to the desired outcomes to ensure for streams a) cool waters (e.g., temperature <15 C year round); b) little or no sedimentation; and c) input of large woody debris over the long haul. These are essential elements not only for amphibians but also for a host of other biota (stream invertebrates to salmonid stocks) that depend on the same suite of stream conditions. Our barometers or indicators can be accurate tracking of stream temperatures (via automated recorders that are now relatively inexpensive) and rapid habitat assessment (as siltation is obvious to the trained eye).

We need to better determine the occurrence and abundance of aquatic biota across major climatic gradients. There are generally cooler conditions from south to north, inland to coast, and from low to high elevation. Impacts from timber harvest may be ameliorated or less severe in northern, maritime, or high elevation as opposed to southern, interior or low elevation locales. We may find that buffer widths can be less wide in streams subjected to maritime conditions than sites located farther inland. We really do not know right now.

Still, stream temperatures in harvested stands may increase to harmful levels for the critical period of egg survival for stream amphibians. We know the maximum tolerance level for only one of the three stream amphibians groups: eggs of the tailed frog perish at 18.5 C. There may be sublethal effects at lower temperatures. Again, we lack data.

Intermittent streams or headwaters are often overlooked in forest management plans, but these are critical to the survival of stream amphibians and for maintenance of stream conditions downstream that include the economically important salmonid fishes. Preliminary studies in the Umpqua River basin in southern Oregon (Bury, pers. obs.) indicate that tailed frogs and torrent salamanders are restricted to headwaters that are stream order 1-2 (basically <2m). Tailed frogs and giant salamanders may occur down to third order waters and, rarely, larger waters. We lack information on the

distribution of herpetofauna along streams in other areas along river continua. We have no studies on how logging affects large-stream biota that include the yellow-legged frogs and Western pond turtles.

Substrate and parent geology appear to be important to presence of stream amphibians. Although we have tended to debate the role of marine deposits, the bigger question is the amount of sedimentation that is occurring in any watershed. Although in need of better documentation, the key here is maintenance of streams with interstitial spaces that may be essential to survival of many stream amphibians.

Nesting areas of stream amphibians need protection, but this is difficult because few egg masses have ever been found due to a) their placement under large rocks, boulders or underground seeps; b) communal nesting that concentrates eggs in a few sites; and c) lack of extensive searches. This chapter in their life history is mostly blank.

We need data on the movement patterns, dispersal abilities, and general landscape-level needs of tailed frogs for effective conservation. For example, newly metamorphosed tailed frogs travel upslope but we lack information on how far they travel into forests and how long they spend on land.

In the past, clearcut logging occurred over large areas that tended to fragment blocks of suitable habitat. Continuing timber harvest at these remaining sites may further deplete the remaining populations. Although there are many improved methods of timber harvest (e.g., thinning of stands and retention of riparian reserves), studies are just starting on how these practices may affect amphibians.

We need to determine the effectiveness and cost efficiency of different widths of buffer zones along streams to protect aquatic organisms. Thinning of stands is increasingly used as a management tool to harvest timber and to reduce fuel loads, but there are few or only small-sized treatments in the region. Wide-scale implementation of thinning of forests needs further consideration and review.

6.3 Macroinvertebrates

Nicole M. Czarnomski
Oregon State University, Department of Forest Science
321 Richardson Hall
Corvallis, Oregon 97331

6.3.1 Introduction

Aquatic invertebrates play many key roles in the stream ecosystems of the Pacific Northwest. They are the major consumers of detrital input from the riparian area and are often abundant when food sources are available (Hawkins and Sedell 1981; Gregory et al. 1991; Naiman and Anderson 1997). In streams in relatively undisturbed forests, aquatic invertebrate diversity is extensive and abundance remains generally stable (McElravy, Lambert, and Resh 1989; Richards and Minshall 1992). In a modest sampling effort over a hundred different species may be detected (Hershey and Lamberti 1998). In addition, they are prey species for many aquatic vertebrate species including salmonids and amphibians (Moring and Lantz 1975; Wipfli 1997), as well as terrestrial vertebrate species. According to the Oregon-Washington Species-Habitat Project database (O'Neil et al. 2001), 196 species of amphibians, reptiles, birds, and mammals use aquatic invertebrates as a food resource.

Major taxa of aquatic invertebrates of the Pacific Northwest include: *Ephemeroptera* (mayflies), *Odonata* (damselflies, dragonflies), *Plecoptera* (stoneflies), *Megaloptera* (dobsonflies, alderflies), *Tricoptera* (caddisflies), *Coleoptera* (beetles), *Collembola* (springtails), *Diptera* (true flies), *Gastropoda* (snails), *Decapoda* (crayfish), and *Amphipoda* (amphipods) (Moring and Lantz 1975,

Porter and Meehan 1987, Hershey and Lamberti 1998). Few species appear on any “sensitive species” short list because most are both relatively widespread and frequent.

Life histories are highly varied according to seasonal fluctuations, life cycle length, and developmental strategies (McIntire and Colby 1978; Anderson and Sedell 1979; Hawkins and Sedell 1981; Porter and Meehan 1987; Progar and Moldenke 2002). Temperature and photoperiod associated with seasonal change play a role in determining when a particular species may emerge, transition from a larval to adult stage, or export downstream (Porter and Meehan 1987; Piccolo and Wipfli 2002). In the Pacific Northwest, many species overwinter in a larval stage and synchronize their emergence in order to increase the probability of finding mates (Hershey and Lamberti 1998). During much of the summer, more than 100 insects may emerge from a single square meter of stream per week (Progar and Moldenke 2002). In four geographical areas of study in Oregon, *Diptera* was the most abundant order collected in summer and fall and *Ephemeroptera* were most abundant in the winter (Porter and Meehan 1987).

Composition and abundance of aquatic invertebrates are largely dependent on sources of available organic matter (Murphy and Hall 1981; Bilby and Bisson 1992; Naiman and Anderson 1997), canopy structure (Gregory et al. 1991; Richards and Minshall 1992; Progar and Moldenke 2002), water quality (i.e., dissolved oxygen) (Gibbons and Salo 1973; Hershey and Lamberti 1998), local geomorphology (Naiman et al. 1992), and basin position (Vannote et al. 1980; Naiman et al. 1992). The River Continuum Concept suggested that the types of invertebrate feeding functional groups located in the stream are related to the location in the stream network, because of changes in the riparian canopy and the relative influences of riparian-derived (allochthonous) vs. internally produced (autochthonous) carbon. Many studies in the Pacific Northwest are consistent with this view (Vannote et al. 1980; Hawkins and Sedell 1981; Hawkins, Murphy, and Anderson 1982; Anderson 1992). Hawkins and Sedell (1981) found that low-order streams with at least partial canopy closure often have aquatic invertebrate composition consisting of 30-50% shredders. In western Oregon, third through fifth order streams create better habitat for collectors and grazers as a shift from heterotrophy to autotrophy occurs due to increases in light and algal production, increases in broken down coarse organic matter, and as stands become dominated more by *Alnus rubra* and *Populus trichocarpa* (Swanson et al. 1982). In general, terrestrial and aquatic interactions decrease with increasing stream size (Swanson et al. 1982).

Substrate and velocity help determine which species will be present in a particular stream reach. Coarse substrate provides better interstitial habitat than fine sediments. For example, water penny beetles, hellgrammite larvae, perlid stoneflies, and case-building caddisflies use the undersides of rocks (Hershey and Lamberti 1998). Large wood and leaf packs are “hot spots” of invertebrate activity because they can be both substrate and a nutritional resource (Anderson and Sedell 1979; Hershey and Lamberti 1998). Only specialized aquatic invertebrates ingest large wood directly, such as cranefly larvae (*Lipsothrix*) and the elmid beetle (*Lara avara*) (Wallace and Anderson 1996). A far larger proportion of aquatic invertebrates feed on the microorganisms that coat the wood (Anderson and Sedell 1979; Bilby and Bisson 1998).

Disturbance effects are dependent on the nature and magnitude of the event, geomorphic and hydrologic stream characteristics (Resh et al. 1988), and community structure (Minshall et al. 1985). The intermediate disturbance hypothesis predicts that the greatest aquatic invertebrate diversity will occur at intermediate levels of disturbance. At low disturbance levels, large, longer-lived invertebrates dominate communities; while at high disturbance, those species that have poor colonization mechanisms or are long-lived are excluded, leaving small, short-lived invertebrates (McAuliffe 1984; Hershey and Lamberti 1998). Flow variation (from floods to desiccation) can be responsible for large, often temporary, decreases in abundance and diversity (Lamberti et al. 1991). Large wood reduces shear stress during high discharge events, helping to stabilize the substrate

(Naiman and Anderson 1997). The hyporheic zone can provide refuge and source for colonizers, but is usually only available to smaller invertebrates (Stanford and Ward 1992; Naiman and Anderson 1997; Edwards 1998).

In the Pacific Northwest, mechanisms for aquatic invertebrates to recolonize stream reaches after a natural disturbance include downstream drift, drift from tributaries, upstream flight, flight from other watersheds, upstream swimming, upstream crawling, and movement from hyporheic refugia (Hershey and Lamberti 1998, adapted from Smock 1996).

6.3.2 Ecological Processes and Habitat Features Related to Forestry Practices

Effects from clearcut logging on the stream ecosystem include the introduction of sediment, removal of leaf litter and other organic inputs, and the change in flow, temperature, and nutrient composition (Gibbons and Salo 1973; Murphy and Hall 1981; Swanson et al. 1987; Gregory et al. 1991), altering energy flow from terrestrial to aquatic habitats (Murphy and Hall 1981; Wipfli 1997). Open canopied streams showed higher abundances of aquatic invertebrates and increases in the abundance of all the feeding functional groups besides shredders, which remained relatively stable, compared to streams with closed forests over them (Hawkins, Murphy, and Anderson 1982). In the Oregon Cascades, the clearcut section had four times the insect emergence, although biomass was relatively the same (Grafius 1976).

Canopy vegetation composition is more influential than substrate in determining total abundance and trophic levels present in the stream (Hawkins, Murphy, and Anderson 1982). The count and biomass density of aquatic invertebrates were found to be 3 times greater in 35- to 40-year-old red alder sites than in 35 to 40 year old conifer sites (Piccolo and Wipfli 2002). Aquatic invertebrate abundance has been found to be higher in *Alnus rubra* stands than stands dominated by *Thuja plicata* or *Tsuga heterophylla* (Kolodziejczk and Richardson 2001). Deciduous tree leaves that are high in nutrients (e.g., alder and maple) are broken down within four to six months, while leaves from other deciduous tree species (e.g., oak), conifer needles, and shrubs and herbs with waxy cuticles (e.g., willow and sword fern) may take 1 to 2 years (Gregory et al. 1991).

There are no studies that directly relate size of forest harvest areas to stream conditions for aquatic invertebrates. Primarily, studies have been conducted on stream reaches that are relatively short (100-300 m). Robinson and Minshall (1986) have stressed the need to compare a variety of patch sizes to get a more accurate understanding of aquatic invertebrate response.

In early succession, species richness is highest, which drops to a lower number of species once the canopy is closed, then eventually returns to intermediate levels of aquatic invertebrates as the canopy ages (Franklin 1992; Triska, Sedell, and Gregory 1982). Murphy and Hall (1981) found that predatory insects in the Oregon Cascades showed that species richness was 28% greater and biomass was 88% greater in clearcut than in old-growth sites, yet communities were predominantly stoneflies. Their densely shaded second-growth sites contained fewer predatory aquatic insects than old-growth or clearcut sites. However, Anderson (1992) found that when comparing insect taxa at three sites in the Oregon Cascades, there was no significant difference: old-growth had 196, the 5-year-old clearcut had 191 and the 40-year old deciduous (primarily alder) had 165. It is important to note that the 40-year-old deciduous site experienced a debris flow within 10 years of the study, but many of the aquatic insects had recolonized.

Aquatic invertebrate abundance recovers relatively quickly from openings in the canopy (Murphy and Hall 1981; Anderson 1992), but diversity does not recover as quickly (Erman, Newbold, and Roby 1977; Newbold, Erman, and Roby 1980). Newbold, Erman, and Roby (1980) found that although overall density was significantly higher in streams logged without buffers than in unlogged streams, diversity was significantly higher in unlogged streams. Results from streams with narrow buffer strips

were too varied to show a significant difference than either unbuffered or unlogged, but with a buffer of 30 m, they determined there was no significant difference in aquatic invertebrate populations compared with unlogged reaches.

Other important aspects in considering logging frequency are the rate of recovery of large wood that can enter the stream (Murphy and Hall 1981), and the frequency of shifting in substrate materials that can alter food abundance and aquatic invertebrate communities (Robinson and Minshall 1986).

Tree species composition and canopy structure alter the composition and abundance of aquatic invertebrates (Gregory et al. 1991; Koloziejczyk and Richardson 2001). Low, dense canopies allow little sunlight for primary production, whereas high, more open canopies allow some light through (Murphy and Hall 1981; Gregory et al. 1991). In a study in the Oregon Cascades where clearcutting and burning occurred next to a stream without a buffer, Murphy and Hall (1981) found that density of aquatic invertebrate taxa increased more in riffles than in pools because of increased primary production and less sedimentation.

Logging practices have altered the size and amount of large wood in the stream ecosystems of the Pacific Northwest (Sullivan et al. 1987; Bilby and Ward 1991; Benda, Bigelow, and Worsley 2002). Riparian buffers have protected some of the large wood inputs (Gregory and Ashkenas 1990), and it has been suggested that riparian buffers may increase the amount of wood entering the stream in the short term due to windthrow (Hairston-Strang and Adams 1998). Removal of large wood serves to simplify habitat or increase sediment loading which can reduce aquatic invertebrate density (Niemi et al. 1990).

Watershed or larger scale considerations. One of the reasons it is difficult to quantify how disturbance affects aquatic invertebrates is because disturbance operates at varied spatial scales that range from an individual rock to an entire watershed and broad temporal scales from a single event to long successional time periods (Gregory et al. 1991; Naiman and Anderson 1997).

Canopy type significantly alters quantity and biomass of aquatic invertebrates exported downstream (Piccolo and Wipfli 2002); therefore, timber harvest in the headwaters is expected to alter riparian inputs and the energy flow through the food web (Triska, Sedell, and Gregory 1982; Wipfli and Gregovich 2002). In southeast Alaska, it has been found that every 1 km of salmon-bearing stream has the potential to receive enough food resources, by means of aquatic invertebrates and detritus, from non-fishbearing headwater streams to support 100-2000 young-of-the-year salmonids (Wipfli and Gregovich 2002).

Road building associated with logging has the potential to decrease aquatic invertebrate abundance and diversity by altering peak flow in streams (Jones and Grant 1996; Jones 2002) and increasing the frequency and severity of landslides and debris flows in the Pacific Northwest (Swanson et al. 1987). Lamberti et al. (1991) found that 99% of macroinvertebrates were removed by a debris flow in the Oregon Cascades, while the flood alone removed 90% of the species. In the same region, Anderson (1992) found that most aquatic insects are able to recolonize debris flow opened habitat within a few months, and herbivore shredders and piercers were the most affected by the debris flow.

Regional variation. There is a large diversity of habitats in the Pacific Northwest; therefore, seasonal emergence varies depending on region. A study conducted by Porter and Meehan (1987) in four regions of Oregon (Coastal, Cascades, Central, and Eastern) determined that in most areas and seasons, *Diptera* and *Ephemeroptera* combined comprised over half of all stream invertebrates collected. High percentages of mayflies were found in Coastal and Cascades Oregon in the spring, while high amounts of both mayflies and stoneflies were found in Eastern Oregon and springtails were more abundant in Central Oregon.

Timing and magnitude of flood flow can vary from coastal to inland regions, scouring bed materials and depleting aquatic invertebrate populations (Naiman and Anderson 1997; Hershey and Lamberti 1998). In coastal streams and the Cascades, rain-on-snow events can produce high flow events that reset the stream biota (Lamberti et al. 1991). Debris flow frequencies vary among regions (Swanson et al. 1987), and are often triggered by large precipitation events, exacerbating impacts of a flood on aquatic invertebrates.

6.3.3 *General Guidelines for Sustainable Forestry Practices*

We don't yet know much about the impacts of specific buffer widths and current forest management practices on aquatic invertebrates, but studies are underway. The most influential elements of the riparian area on aquatic invertebrates include canopy cover, litter and organic input, and the input of large wood. Riparian management practices should take into account these needs and the influence of the headwater streams. In addition, because of the large amount of information on aquatic invertebrate responses to environmental conditions, many responses can be used as indicators of stream conditions (Naiman 1998; Hershey and Lamberti 1998).

6.3.4 *Information Needs*

The relationship between the terrestrial ecosystem and the stream ecosystem is well understood qualitatively, but not quantitatively (Hershey and Lamberti 1998). The role of disturbance to the riparian canopy structure needs to be further examined. Aquatic invertebrate biodiversity appears to increase as patches are opened by disturbances (Section 2.3) that increase habitat heterogeneity (Anderson 1992). More studies need to be done on how the frequency and intensity of logging and associated road building influence dispersal, rate, and speed of recovery of aquatic invertebrate populations (Jones et al. 2000). The functionality of riparian buffer widths at maintaining diversity and population densities of both aquatic and terrestrial-riparian arthropods needs to be assessed in both the mesic forests of the north and the more xeric forests of the south (see research of Rykken and Moldenke, Oregon State University, unpublished).

Many studies have been conducted in the coastal region and the Cascades, but more studies need to be initiated in the interior like those conducted in central Oregon by Progar and Moldenke (2002). These have documented that a) temporary headwater streams produce higher densities of invertebrates (i.e., migratory bird food) than continuous flow primary streams; b) continuous flow primary streams have higher levels of diversity/species richness than temporary ones; and c) the unique species in the temporary streams are not true aquatic species, but are related to terrestrial-riparian species.

The linkages between aquatic invertebrates and vertebrate species should be of interest to managers and have not been well studied. In the short term, there is a need to carefully consider the often opposing needs of both salmon and terrestrial birds/bats for the food resource provided by aquatic insects. For example, very few hard data have been collected about the diel flight periods of the major species of aquatic insects (bat food versus bird food) (Alex Farrand, Department of Fish and Wildlife, Oregon State University, unpublished data).

7.0 FORESTRY PRACTICES AND TERRESTRIAL BIODIVERSITY

7.1 Vascular Plants

Robert J. Pabst
Faculty Research Assistant
Oregon State University Department of Forest Science
Corvallis, Oregon 97331

Daniel A. Sarr
Klamath Network-National Park Service
129 Central Hall
Southern Oregon University
Ashland, Oregon 97520

7.1.1 Introduction

Vascular plant distributions are governed by the availability of critical resources for growth, suitable temperature conditions for photosynthesis and growth, and availability of growing space. Most vascular plants require comparable growth resources, including mineral nutrients, water, and with the exception of a few saprophytic species, light. High levels of specialization for unique or even transient combinations of these resources are typical of most flora and this is especially true for riparian forests. Spatial gradients in resources (light, soil moisture), stress (flooding) and temporal gradients caused by disturbance are well exploited by riparian plant species, yielding high diversity. Species and life form groups vary sharply in their tolerances to the various physiological stresses imposed by the riparian environment. Ephemeral species are well represented in well-illuminated, spatially complex, and frequently flooded streamside environments (Pabst and Spies 1998). These conditions are more stressful for longer lived tree and shrub species, which may show lowest richness next to streams (Sarr 2005). Still other species show strong substrate preferences, and primarily occur on either mineral or organic substrata (Minore and Weatherly 1994; Pabst and Spies 1998). In short, the diversity of plant species is driven by the spatial and temporal complexity of the riparian environment.

An array of local and regional processes creates this complexity and provides opportunities for plant establishment and development. Local processes include erosion and deposition associated with fluvial disturbances, colluvial processes such as raveling and slope failure that bring organic and inorganic materials from uplands to the riparian area, the dispersal of propagules into and out of the riparian zone by various means, periodic fire, and biotic interactions among plants as well as among plants and animals. At larger scales, history, climate, geology, and watershed processes govern the spatial distributions of plant species in the Pacific Northwest (Whittaker 1960; Waring and Major 1964; Waring 1969; Zobel, McKee, and Hawk 1976; Ohmann and Spies 1998; Wimberly and Spies 2001).

Riparian forests harbor a high diversity of understory plant species, some of which are unique to the streamside environment and many others that also occur in the uplands (Mouw and Alaback 2003). The assembly of riparian communities is determined in part by environmental gradients that vary and interact at multiple spatial scales (Baker 1989; Bendix 1994). Climatic gradients and geologic substrata may control what plant species are found at the landscape scale (Sarr 2005). For example, salmonberry (*Rubus spectabilis*) is widespread at lower elevations in western Washington and in Oregon's Coast Range, where it occurs along streams as well as in the uplands, but in drier westside locations (i.e., eastern and southern Coast Range, Cascades, and Siskiyou Mountains) it is absent or its extent is limited to streamsidess (Sarr 2005). Woody plant diversity has been shown to vary

strongly along landscape climate gradients coincident with changes in upland floras (Collins, Risser, and Rice 1981; Sarr 2005). West of the Cascades, woody plant richness typically is lowest in the wettest most productive environments, where canopy densities are greatest and topographic moisture gradients are most muted (Sarr 2005). Studies of upland forests suggest that herbaceous plant diversity shows a similar pattern (Whittaker 1960), but a regional study has yet to be implemented that addresses total plant diversity in riparian environments.

Within watersheds, the composition of riparian plant communities changes as stream gradient, valley floor width, and the complexity of valley bottom landforms change from the upper to lower reaches of a stream network (Hupp 1986). This has been demonstrated in both the Oregon Cascades (Campbell and Franklin 1979) and the Oregon Coast Range (Pabst and Spies 1999). In addition, total species richness, as well as the proportion of exotic and pioneer species, has been shown to increase from the upper, constrained reaches of the McKenzie River in Oregon to the piedmont zone where the river gradient lessens and the valley floor widens (Planty-Tabacchi et al. 1996; Tabacchi et al. 1996).

At the scale of stream reaches, variability in plant communities is associated with elevation above the stream and other factors related to it, including susceptibility to flooding, soil moisture, soil texture, site productivity, and microclimate. Microclimate has not been directly associated with plant community composition in the Northwest, but has been shown to change relative to buffer widths in both western Washington (Brososke et al. 1997) and northwestern California (Ledwith 1996a, 1996b). Along a stream-to-hillslope gradient in the central Coast Range of Oregon, species richness and diversity of understory vegetation were higher on valley floors than on lower hillslopes; within the valley floor, more frequently disturbed areas such as active floodplains and vegetated gravel bars were more species-rich than less disturbed areas such as terraces and seeps (Pabst and Spies 1998). In contrast, Sarr (2005) noted lower diversity of woody plants on floodplains than adjacent hillslope forests, despite greater geomorphic complexity on the floodplains. These contrasts may be due partially to differences in physiological tolerances of herbs and woody plants, as well as to the fact that understory diversity is typically highest where environmental conditions limit dominance by trees and tall shrubs.

Microhabitats such as back channels, seeps, depressions, and boulders or logs in or near the stream provide unique environments for plants and introduce finer-scale heterogeneity in the riparian understory (Campbell and Franklin 1979; Pabst and Spies 1998). Understory composition in the Coast Range changed along the stream-to-hillslope gradient in relation to landform type, topographic position, and coniferous tree cover (Minore and Weatherly 1994; Pabst and Spies 1998). Similarly, distinct plant communities were identified along an elevation/disturbance gradient along streams in the Oregon Cascades (Hawk and Zobel 1974; Campbell and Franklin 1979). The distribution of these communities was further differentiated by substrate texture and corresponding moisture stress (Hawk and Zobel 1974). In the Hoh River Valley on the Olympic Peninsula, vegetation succession was associated with landforms of different ages and elevations that were defined by historical flooding and deposition (Fonda 1974). Riparian plant associations in the national forests of central Oregon are also tightly linked to landform (Kovalchik and Chitwood 1990).

Diversity/equitability patterns and community patchiness in riparian areas are strongly influenced by major disturbances such as floods and debris flows. Scour and deposition from these events create a variety of new substrata and landforms for the establishment of opportunistic herbaceous and woody pioneer species, including non-natives (Gecy and Wilson 1990, Pabst and Spies 2001). Propagules (seeds, spores, vegetative parts) for these plants may have been dispersed by wind, animals, carried by the stream itself (Johansson, Nilsson, and Nilsson 1996), or germinated from the seed bank in the soil. Other species survive catastrophic disturbance by resprouting from buried rootstocks or rhizomes (Gecy and Wilson 1990; Pabst and Spies 2001) or by being flexible or resistant to the force of peak flows. Composition of the riparian seed bank was evaluated on three types of alluvial surfaces along

streams in the central Cascades of Oregon (Harmon and Franklin 1995). Seed banks were dominated by herbaceous species, with nearly 77% of the species not represented in the existing aboveground vegetation. This indicates the potential for an expansion or shift in species composition in riparian areas following disturbance. Species abundance and richness of the seed bank were higher on vegetated gravel bars that experienced occasional fluvial disturbance than on surfaces disturbed more or less frequently (Harmon and Franklin 1995). This trend associating richness or diversity with disturbance intensity or frequency has been documented elsewhere as well. For example, in southeast Alaska, species richness was highest in areas with intermediate frequency of flooding and a high degree of spatial variability in flood frequency (Pollock, Naiman, and Hanley 1998). In contrast, richness was found to increase with increasing flood severity in southern California (Bendix 1997). Community patchiness along streams is further enhanced by local disturbance events such as windthrow of overstory trees and small slope failures, which increase the availability of light and possibly soil moisture for plants.

Biotic interactions also influence the composition of riparian plant communities. Competition among plants for light, moisture and nutrients is an important force in the organization of plants and communities, while herbivores such as beaver (Wright, Jones, and Flecker 2002), elk, deer (Liang and Seagle 2002), and mountain beaver (Neal and Borrecco 1981) can dramatically affect the makeup and stature of the riparian understory. Beaver-impounded sites in the Coast Range host a unique assemblage of graminoid species at the water's edge, making these sites compositionally distinct from unimpounded sites and debris jams, leading to greater biodiversity in the landscape (Perkins 2000). Competitive effects appear to be the reason for lower species diversity in red alder/salmonberry community types in the Coast Range, compared with other community types associated with alder (Carlton 1989). Furthermore, species richness within the alder/salmonberry type did not change across different successional stages (i.e., over time) (Henderson 1978). It has been hypothesized that dense cover of shrubs, particularly salmonberry, limits the regeneration of conifer tree species along streams in the Coast Range of Oregon (Carlton 1989; Hibbs and Giordano 1996; Hibbs and Bower 2001). However, in a controlled experiment in western Washington, Beach and Halpern (2001) found that seed source availability (as a function of dispersal distance) was the primary factor governing conifer regeneration, and that competitive interactions and substrate type were of secondary importance. This has implications for riparian understories since the presence or absence of conifers and the year-round shade they cast affect plant community composition (Pabst and Spies 1998).

7.1.2 *Ecological Processes and Habitat Features Related to Forestry Practices*

Only a few studies directly examined the effect of forest practices on vascular plant diversity in the understory of riparian forests in the Pacific Northwest. Therefore, in addition to summarizing these studies, we also reviewed findings from studies outside the region or in upland areas. In many cases, the studies did not explicitly address questions of disturbance intensity, size, frequency, or proximity to stream, so these findings represent only a partial description of the effects of harvest on vascular plant diversity.

The Washington Department of Natural Resources undertook a study to determine how different methods of riparian forest management affected wildlife and vegetation in low elevation, second growth, conifer-dominated riparian forests in western and northeastern Washington (O'Connell et al. 2000). Sampling was done two years before and two years after clearcut harvest in the adjacent uplands to compare current (mid 1990s) riparian forest protection rules ('state' treatment) with 'modified' (more protective) rules, and an unharvested control. The state and modified rules included a no-entry zone as well as some selective cutting in the riparian buffer. Multiple sites were selected for each treatment along Type 3 (fish bearing) or Type 4 (perennial, non-fish bearing) streams. An apparent drawback in the study design was that treatments were not replicated at the site level; that is, each site received a different treatment, possibly confounding site effects with treatment effects.

Results from the western Washington sites show that prior to harvest, cover of mosses, ferns, deciduous shrubs, and berry-producing shrubs was significantly greater in riparian areas than in uplands. Following harvest, the cover of ferns and mosses in the riparian zone was significantly greater in the control sites than in the treated sites. However, cover of berry-producing shrubs was significantly greater in riparian zones bordered by clearcuts, possibly in response to increased light from the uphill edge. At the northeastern Washington sites, the pretreatment comparison between riparian and upslope vegetation showed that the riparian areas had significantly lower richness of shrub species, significantly higher richness of herbaceous species, and that most species occurred in both upland and riparian areas. Following harvest, there was no difference in the richness of shrub species among treatments. Richness of herbaceous species did not differ after treatment in the control or under the modified rules, but was significantly less following harvest under state rules.

In the Oregon Coast Range, Hibbs and Giordano (1996) compared vegetation in red alder-dominated buffer strips to that in alder-dominated riparian forests undisturbed by logging. The buffer strips, ranging from 5 to 50 m wide, represented a chronosequence of time since harvest that ranged from 0 to 32 years. Nearly twice as many herbaceous species were detected in the buffers as in the undisturbed forest, with 22 herbaceous species being unique to the buffers. However, measures of herbaceous species richness, evenness, and diversity did not show a statistically significant difference between buffered and undisturbed sites. Cover of the shrub layer was higher on average in the buffers, with salmonberry showing the most pronounced difference.

Also working in the Oregon Coast Range, Hibbs and Bower (2001) examined understory vegetation in unharvested buffer strips under four overstory canopy types across a chronosequence of time since harvest (from 1 to 33 years). The number of shrub species (richness) was highest in the buffer strips with a conifer cover type, whereas the number of herbaceous species was highest in the mixed, conifer-dominated type. The pure hardwood type had the fewest herb and shrub species. Percent cover of the herbaceous layer did not change with buffer age or with distance from the clearcut edge. Cover of shrubs also showed no association with distance from edge but was significantly (weakly) correlated with buffer age. As part of the same study, Hibbs and Bower (2001) compared their buffer data to that from unmanaged, conifer-dominated riparian forests (Pabst and Spies 1999). They found that total cover of the herb and shrub layers was not significantly different between buffered and unmanaged riparian forests, leading to the conclusion that buffers differed little in composition from undisturbed forest. More detailed comparisons, such as the cover of individual species, total species richness, and the proportion of non-native species, were not made between the two data sets.

Research from outside the region or from upland areas may also shed light on understory response to harvesting. Deal (1997) studied riparian forests in coastal Alaska that developed after 45 years of logging. He found that richness of vascular plants in the understory of alder-dominated or mixed alder-conifer stands was about twice that found in a conifer-dominated stand. In upland forests of the Pacific Northwest, species richness increased with thinning intensity in Washington (Thomas et al. 1999) and Oregon, although in the Oregon study, a portion of the increase was due to the presence of non-native species (Bailey et al. 1998). Conversely, He and Barclay (2000) found no significant effect of thinning and fertilization on vascular or nonvascular species richness in the understory of a young Douglas fir stand 27 years after treatment. In the coastal redwood forests of northern California, species richness increased in association with a sunlight gradient from within 30-50 year-old regenerated clearcuts (low light) into old-growth forests (higher light) (Russell and Jones 2001).

Tree harvesting adjacent to or within riparian buffers could influence the composition and structure of vegetation in the buffers, given the potential for disturbance to soils, increased rates of windthrow of overstory trees (Steinblums, Froehlich, and Lyons 1984), and changes in the light regime and microclimate (Brososke et al. 1997; Ledwith 1996a, 1996b). Existing evidence from the Pacific Northwest does not give clear support for this hypothesis (O'Connell et al. 2000; Hibbs and Giordano

1996; Hibbs and Bower 2001). Hibbs and Bower (2001) speculated that edges created by upslope harvesting in the Coast Range are mitigated by rapid growth of the vegetation, although in less productive climates of the Pacific Northwest (e.g., east side of both Cascades and Klamath Mountains; Appendix A) it is likely that functional regrowth of vegetation would take longer. It is plausible that plant species that are adapted to the dynamic riparian environment are not particularly sensitive to changes in resource availability brought about by upslope logging. For instance, Bendix (1998) postulated that valley bottom plant communities may be in a relatively stable ‘quasi-equilibrium’ with disturbance from the flood regime. However, herbaceous plants in riparian areas respond to finer-scale environmental variability than the shrub and tree layers (Decocq 2002).

Roads and logging also have been associated with higher rates of erosion and sedimentation (Hagans, Weaver, and Madej 1986) and possibly increased incidence of debris flow (Robison et al. 1999) and the volume of sediment they entrain (Johnson, Swanston, and McGee 2000), all of which have the potential to alter streamside plant communities. Yet we know of no study that has attempted to link these dynamics to vascular plant diversity.

Regional Variation. We know of no studies that have examined a consistent set of harvest techniques in riparian forests across the region, but other field studies may provide important insights into potential effects of forest management. Sarr (2005) studied woody plant diversity in forest interiors and disturbance gaps in riparian forests of four watersheds ranging from the wet western Coast Range through the western Cascades to the dry eastern Siskiyou Mountains in southwestern Oregon. He found that gaps had significantly higher woody plant richness than forest interiors in the Cascades, but differences were not significant in the wettest and driest climates. In the wettest climate, salmonberry dominance limited diversity in gaps, whereas in the driest climate the relatively open forests were of comparable richness to gaps. Parallel comparisons of species composition between gaps and forest interiors at the sites suggested that differences in plant composition were associated with increased light availability with disturbance in wet climate riparian forests, whereas in the driest climate, disturbance caused a shift toward more drought-tolerant taxa. The implications of this study for forest management may be that disturbances of similar sizes may lead to different vegetation responses in sharply contrasting climates, as the relative roles of light limitation, microclimatic stress, and shrub competition change.

7.1.3 General Guidelines for Sustainable Forestry Practices

Because vascular plant species show strong differences in microhabitat specialization, land managers can protect biodiversity by maintaining heterogeneity in vertical and horizontal stand structure. They should also take care to avoid damage to unique intra-riparian habitats or substrata that contribute to habitat heterogeneity and presence of legacies. Examples include snags, downed logs, boulders, seeps, depressions, back channels, beaver ponds, and mountain beaver dens. Furthermore, the “quality” of riparian vegetation—in terms of the presence and proportion of native versus non-native species—must be considered when evaluating potential impacts of logging and roading. Roads can be conduits for the spread of non-native plant species (Trombulak and Frissell 2000) as well as pathogens (e.g., *Phytophthora*) (Jules et al. 2002). Some highly invasive, non-native plant species are particularly troublesome in riparian areas, with the ability to form monocultures at the expense of native plants. Examples include Himalayan blackberry (*Rubus discolor*), reed canarygrass (*Phalaris arundinacea*), false brome (*Brachypodium sylvaticum*), butterfly bush (*Buddleia davidii*), creeping buttercup (*Ranunculus repens*), and Japanese knotweed (*Polygonum cuspidatum*) (Native Plant Society of Oregon, http://www.emeraldnpso.org/PDFs/Invas_Orn.pdf). Although it is certain that natural forests historically experienced disturbance of a wide spectrum of intensities, moderate or low disturbance may currently be warranted in watersheds known or suspected to have high potential for non-native plant invasion.

In summary, the effects of timber harvest on vascular plants appear to be variable and dependent upon life form group and site characteristics such as climate and existing vegetation type. Because many vascular plant species show broad associations on disturbance gradients (Spies and Turner 1999), differences in species richness between different silvicultural treatments and stand ages are often nonsignificant. In addition, since many studies are retrospective stand comparisons, it is unknown if differences noted are due to site or treatment. Some tentative conclusions seem appropriate: a) vascular plant species diversity as a whole is not strongly affected by harvest, but silviculture will affect vegetation composition; b) non-native species increase in proportion with disturbance and vegetation quality may decline; c) more open disturbed, old-growth, or deciduous forests may have somewhat higher diversity than young even-aged conifer stands.

7.1.4 Information Needs

Even these broad summary statements require considerably stronger substantiation. A more consistent application of specific treatments replicated across landscape gradients of the Pacific Northwest may be needed to clarify the effects of riparian management on plant diversity in different locales. Other potential research topics include the following:

- 1) Conduct a before/after control treatment study of harvesting effects on understory vegetation in Oregon and northern California. Ideally, this type of study would be stratified across a range of stream sizes and stand types, with treatments replicated at each site, and sampling conducted over a long time frame. Attributes to measure/monitor would include cover (preferably biomass) and constancy of all plant species, disturbance, light regime and soil moisture, etc. This would considerably strengthen the findings of existing retrospective studies. Treatments might include variable thinning approaches, small patch cutting, and shelterwood harvest with variable green tree retention levels.
- 2) Develop successional models to simulate vegetation development in riparian (and upland) areas following disturbance. A greater understanding of the life history of many riparian plants is needed to develop a predictive basis for determining forest management effects on riparian plant diversity.
- 3) Understand the factors driving the distribution of key native and non-native plant species in riparian areas. We lack basic information on the distributions of most native riparian species on geographic, hydrologic, or disturbance gradients. A gradient perspective of riparian vegetation may allow researchers to extrapolate from geographic areas where research has been most intensive (e.g., Oregon Coast Range) to areas where studies are sparser. In addition, we need an empirical and predictive basis for understanding non-native species distributions and to estimate their responses to different management techniques.
- 4) Conduct additional chronosequence studies of riparian buffers, similar to that of Hibbs and Bower (2001), in areas outside the Oregon Coast Range. Successional trajectories vary sharply depending upon such geographic factors as climate, species present, so more geographic coverage is needed to evaluate the generalities of such local findings.

- 5) Examine how riparian restoration efforts affect plant communities. In many areas of the Pacific Northwest, geomorphic alterations due to loss of large woody debris or beaver, non-native species invasions, or other changes have led to degraded vegetation condition. It is unknown if such changes can be reversed through vegetation planting, large wood emplacement, or non-native plant eradication. More work is needed to determine the feasibility or impact of such restoration efforts.

7.2 Non-Vascular Plants

Jeff Shatford

Department of Forest Science, College of Forestry
Oregon State University
Corvallis, Oregon 97331

7.2.1 Introduction

The humid temperate rainforests of the coastal mountains are typified by the luxuriant growth of lichens and mosses, both on the forest floor and as epiphytes on live trees and snags. Bryophytes (mosses, liverworts, and hornworts) and lichens (dual organisms, individuals of which are composed of an alga and a fungus) represent two widely disparate groups with similar habitat preferences in forests of the Pacific Northwest. For simplicity, when referring to these two groups collectively, I will refer to them as nonvascular plants for the remainder of this section. As photosynthetic organisms, nonvascular plants not only comprise an important element of riparian biodiversity, but they contribute functionally to carbon fixation, and in the case of cyanolichens, to nitrogen fixation in riparian ecosystems. I discuss here basic lichen and bryophyte biology as it relates to the vascular plant community (trees and shrubs), and the riparian ecosystem as a whole.

Non-vascular plants play a major role in forest ecosystems, capturing and converting light (primary productivity). Lichen biomass may exceed 1 metric ton per hectare and bryophytes several times this (McCune 1993, and references in Longton 1992) reaching their greatest abundance in oceanic regions (Schofield 1984). They function to filter air and water, and they are major contributors of nitrogen and carbon to the terrestrial and aquatic food webs. They serve as food for a variety of vertebrates (including elk and flying squirrels) and invertebrates, as well as nesting material for birds and small mammals. They act as sources and sinks for nitrogen and in contact with water they act as filters and sponges to absorb nutrients in terrestrial and aquatic settings.

The narrow habitat requirements of some non-vascular plants, where they are known, make them valuable indicators of the forest type or environmental conditions (e.g., soil pH, Klinka et al. 1995). Some are associated with particular substrate types, be it rock, bark, wood, soil, etc., which helps to identify them and in turn has led to their use as environmental indicators. In Europe, bryophytes are frequently used to classify forest types, although this is rarely done in North America (Klein and Vanderpoorten 1997, Klinka et al. 1995).

Basic Biology, Distribution and Diversity. The importance of riparian areas to non-vascular plants arises because of specific habitat features important to non-vascular plants, particularly humidity, light, and substrate. Non-vascular plants typically do best with abundant moisture and light but moderate temperatures, hence their abundance in the moist regions of the coastal temperate rainforests of the Pacific Northwest. They may be restricted to locations where faster growing vascular plants are limited and therefore frequently associated with particular habitats including bare rock, the darkened forest understory, or as epiphytes growing high in the canopy on live or dead tree branches and boles.

In this way they are well adapted to take advantage of the favorable growing conditions in the Pacific Northwest. Although, as noted, they are fundamentally different taxonomically, the lifestyles of bryophytes and lichens are often strikingly similar. Perhaps the most remarkable feature they share is their ability to withstand frequent desiccation, with the ability to resume metabolic activity after rewetting. Generally, nutrients and water may be absorbed over the entire surface of the organism. While advantageous in some ways, this feature makes them sensitive to water borne and air borne pollutants (McCune 2000). The cyanolichens are unique in their ability to fix atmospheric nitrogen, a feature that has likely helped them gain attention among forest managers. Many bryophytes may be tolerant of temperature extremes when dormant, but more heat sensitive when hydrated and undergoing active growth. Respiration rates typically exceed photosynthetic rates at over 25°C, making bryophytes among the most sensitive organisms to increased heat loads in riparian forests (Longton 1980).

Reproduction differs markedly between bryophytes and lichens. Each, however, is capable of sexual and asexual reproduction. The resulting propagules are typically small and dispersed by wind, water, or attached to animals. The reproductive output is often high but survival is more often dependent on the probability of arriving at a site with conditions amenable to growth and establishment (substrate and microclimate).

The accumulation of biomass for non-vascular plants is generally low and highly variable, in comparison to vascular plants. Given adequate time free of disturbance, non-vascular plants may build up considerable biomass, as observed in temperate rainforests throughout the Pacific Northwest. Cool, moist conditions conducive to their growth may occur out of phase with that of vascular plants (e.g., in fall and winter). Even the driest parts of the region, including the interior valleys and mixed forests of northern California, provide abundant habitat for epiphytes and good growing conditions in winter when precipitation tends to be highest. However, riparian zones may be the locations most likely to support bryophyte species that remain active and require appropriate microclimatic conditions through summer (J. Shevock, pers. comm).

Schofield (1988) reports that 85% of the bryophyte species occurring in British Columbia have a Holarctic distribution, whereas the remaining 15% are limited (endemic) to western North America. The Pacific Northwest is recognized as a center of endemism for both lichens (Brodo, Sharnoff, and Sharnoff 2001) and bryophytes (Tan and Pocs 2000) so it is of particular importance to the conservation of non-vascular plant species diversity. Approximately 1000 species of bryophytes occur in the Pacific Northwest: 700 mosses, 300 hepatics (liverworts), and 5 hornworts (Schofield 1984).

Old-growth forests provide conditions for lichens and bryophytes that are unmatched by other forest types due to the continuity of substrates and variety of microsites and microclimates that exist there, from the forest floor upward into the highest part of the canopy (McCune et al. 2000).

7.2.2 Ecological Processes and Habitat Features Related to Forestry Practices

Schofield (1988) suggests that the influences of humans on bryophyte distribution have been less than for vascular plants. The number of introduced species, for example, is limited in quantity and geographic extent. However, indirect impacts on non-vascular plants by humans likely have been extensive. This is primarily through extensive conversion of plant communities that altered habitat availability.

The effects of forest management on non-vascular plant diversity tend to be indirect, by removing habitat structure and substrate heterogeneity and by changing microclimates. The reduction in stand ages and structural diversity has likely had effects on non-vascular plant abundance and diversity, but these effects are currently undescribed. Forest practices may change the microclimates and substrata

available to non-vascular plants, including tree and snag density, abundance of large woody debris on the ground, soil surfaces, vascular plant size and composition. Trees and shrubs provide structure or influence microclimate, or both, for non-vascular plants and, therefore, are primary determinants of habitat suitability. Consequently, it is not surprising that forest practices should impact population viability of non-vascular plants, especially those with narrow habitat requirements. Sillett et al. (2000) point out that many species of lichen, while considered old-growth dependents, do not have narrow habitat requirements, but do seem to be limited by dispersal. Some rare and sensitive lichen species (e.g., *Lobaria oregana*) may require a long time to establish and grow in forests (Sillett et al 2000). Such species appear to be favored by retention of old-growth patches in the landscapes as well as large green trees within managed stands (Sillett and Goslin 1999; Sillett et al. 2000).

Dead standing trees (snags) and large woody debris (LWD) on the ground are important habitat substrates for many non-vascular plants (Jonsson 1996b; Rambo and Muir 1998; Rambo 2001). LWD increases the surface area and heterogeneity of the forest substrata. As the composition of LWD changes over long periods of time, a single piece may, in various stages of decay, serve as habitat for a variety of species and in particular may be more important for non-vascular plants (and fungi) than to seed plants. Live trees, particularly large trees, provide for a wide variety of microclimates as temperature, wind speed, light levels, and humidity all change in various ways from the deep understory to the top of tall trees 60-80 meters into the upper canopy. Bryophytes and lichens are susceptible to changes in humidity brought on by removal of the forest canopy. Some may take advantage of the increase in light availability, although this increase in resources may be short lived as a dense tree canopy develops.

Few studies have attempted to describe non-vascular communities specific to riparian areas (but see Rocky Mountains - Glime and Vitt 1987; Oregon Cascades - Jonsson 1996a, 1996b; McCune, Hutchinson, and Berryman 2002). Bryophytes in particular may take advantage of unique substrata in the near stream environment (the splash zone). Here they may colonize stable boulders or embedded rocks where seed plants may be limited, due to flooding or lack of soil (Englund 1991; Glime and Vitt 1987). Changes in flow regime, sedimentation or debris flows may directly impact the bryophyte community with indirect effects on the aquatic invertebrate community (Englund 1991).

Riparian areas provide a variety of unique characteristics to the larger landscape due to their topographic position. The composition of vascular plants is often highly variable along riparian corridors, where they are subject to frequent disturbance. This may lead to a greater diversity of stand ages and forest types in close proximity, compared to an equivalent area of upslope forest (Naiman et al. 1998). A number of lichen species appear to benefit from the occurrence of hardwoods and associated understory shrubs occupying hardwood stands (Neitlich and McCune 1997; Ruchty, Rosso, and McCune 2001). In a single watershed in Oregon, larger “fish bearing” streams contained a greater number of rare epiphytic lichens (those listed on the survey and manage list—Bureau of Land Management and USDA Forest Service) compared to upland sites or small and intermittent streams (McCune, Hutchinson, and Berryman 2002).

The abundance of hardwood tree species in riparian areas may be an important habitat factor for non-vascular plants. Conifer canopies tend to be dense and carry their needles year-round, making for a darkened understory and mid-canopy. In contrast, deciduous canopies are leafless during winter, when conditions are optimal for bryophyte growth, and understory light levels are higher year-round. The texture and chemical properties of tree bark tend to vary among species and age of individuals, each suited to different kinds of non-vascular epiphytes (Pike et al. 1975).

7.2.3 *General Guidelines for Sustainable Forestry Practices*

The influences of climate, topography, distance from stream, vascular plant composition and age, and abundance of large woody debris on non-vascular plant diversity operate at different scales (Jonsson 1996b) and must be taken into account when managing for particular species or for non-vascular plants as a whole in riparian areas. What is most apparent is the relationship between non-vascular plant abundance and diversity and stand structure (Lesica et al. 1991; Sillett et al. 2000). For the most part, habitat loss has been due to the conversion of older, structurally and compositionally heterogeneous stands to younger, more dense and homogenous forests. Consideration should be given to the amount and distribution of legacy trees and stands to ensure the existence of suitable habitat over the landscape in the long term, and to retention of large green trees within managed stands to serve as sources of propagules to inoculate younger stands (Sillett et al. 2000). In addition to large trees, retention of other legacy features or sources of within-stand heterogeneity including snags, logs, hardwood and shrub patches, and variable density stands, are all factors that may be favorable for maintenance of non-vascular plant diversity in the riparian zone.

7.2.4 *Information Needs*

Despite their abundant growth and diversity, non-vascular plants have rarely received much consideration in forest management in the Pacific Northwest. This has changed to some degree since the implementation of the Northwest Forest Plan. A legacy of neglect is also apparent in the scarcity of personnel capable of identifying non-vascular plants efficiently and accurately. For epiphytic species (i.e., those growing on trees and snags), difficulties also arise in simply accessing the locations where they thrive (e.g., canopies of mature and old-growth forests). The same may also hold true for species growing on cliffs and outcrops over streams and along ridges.

Research on the diversity and conservation of non-vascular plants has developed along various lines of questioning but much remains unanswered. Research has only begun to consider the specific habitat requirements of most species and the trade-offs among life history traits of individual species. Development of an understanding of life history characteristics and habitat requirements, as has been done for some vascular plants, should be part of an adaptive management strategy for maintaining non-vascular species diversity.

The direct harvesting of moss for commercial use has received some attention from research as well (Peck and Muir 2001). Given that riparian areas may be locations of both high diversity (and hence conservation value) and high productivity, there may be some conflict between economic and biological values that warrants further monitoring.

It should be recognized that recent advances in silviculture, especially stand management techniques to increase structural characteristics, are being discussed and implemented to varying degrees (Franklin et al. 2002; Tappeiner, Emmingham, and Hibbs 2002). These methods may favor the persistence of non-vascular plants in managed landscapes, but the short- and long-term implications of such silvicultural techniques have received little attention to date.

7.3 Fungi

Daniel A. Sarr
Klamath Network-National Park Service
1512 E. Main Street
Ashland, Oregon 97520

7.3.1 Introduction

Life History and Ecology. Although the degree of association of most native fungi with riparian areas is poorly understood, maritime forests of the Pacific Northwest have a rich diversity of macrofungi, and they are abundant in riparian forests (Molina pers. com.). Native macrofungi include mycorrhizal, saprophytic, and pathogenic species. Most native conifer and hardwood tree genera form ectomycorrhizal associations with fungi in the Basidiomycotas, Ascomycota, or Zygomycota (Molina et al. 2001). Douglas fir alone may associate with as many as 2000 fungal species across the region. Fungi have tremendous functional importance in forest ecosystems, occurring in the full spectrum of climates, stand types, and successional stages. Many species are essential to decomposition of carbon materials, such as wood and leaf detritus, both in terrestrial and aquatic habitats. Hypogeous sporocarps (truffles) form a major food source for small forest mammals, including the northern flying squirrel (*Glaucomys sabrinus*) (Zabel and Waters 1997). In addition, mutualisms between certain fungi and plant roots (mycorrhizae) have important roles in water and nutrient acquisition for most native riparian trees (Amaranthus and Perry 1987). Pathogenic fungi may also play an important role in maintaining heterogeneity in natural riparian forests by creating small islands of tree mortality and shrub or hardwood establishment.

Aquatic fungi form an essential element of the detrital food web in streams. After leaching of soluble carbohydrates, microbial colonization is the primary form of breakdown of more refractory leaf or stem parts. The layers of aquatic molds that frequently occur on decaying leaves increase the protein content of these substrates, encouraging ingestion by detritivorous insects. Colonization by fungi is rapid and spore densities may exceed 1000 spores /liter (Dix and Webster 1995). Fungi may comprise 63-95% of the microbial biomass on submerged hardwood leaves (Findlay and Arsuffi 1989).

Fungi have evolved to exploit a tremendous wealth of habitats in the Pacific Northwest. Most species of fungi require sufficient seasonal moisture to reproduce. Therefore, fungal reproduction shows high seasonality and interannual variation, depending upon temporal patterns in temperature, precipitation, and relative humidity. In the Pacific Northwest, fungal sporocarp abundance and diversity are believed to be positively correlated with climatic moisture (O'Dell, Ammirati, and Schreiner 1999), reaching peaks in the humid forests of the coastal mountains. Fungi are also positively associated with the presence of large wood and the diversity of decay classes (Molina et al. 2001).

7.3.2 Ecological Processes and Habitat Features related to Forestry Practices

Over 500 species of fungi were identified by the FEMAT process as being closely associated with old growth forest in the Pacific Northwest (Marcot 1997). It is unknown how many are susceptible to forest management of various intensities. The intensity of harvest may be important for fungal diversity primarily through its effect on residual woody debris and soil organic matter. Across gradients of harvest intensity, compositional shifts from forest interior taxa to more disturbance-associated taxa have been noted (Jones, Durall, and Cairney 2003). In a study that transplanted conifer seedlings from forest interiors into forest openings, fewer ectomycorrhizal morphotypes, lower average richness per seedling, and steeper, less even species distribution curves were found on seedlings transplanted into openings (Kranabetter and Friesen 2002). Standing crop of hypogeous (below ground) sporocarps has been noted to be lower in managed stands than in natural-mature and old-growth stands (North, Trappe, and Franklin 1997), and to decrease with the size of the forest

opening (Durall et al. 1999). However, richness and abundance did not appear to differ strongly between mature and old-growth stands on Vancouver Island, B.C. (Goodman and Trofymow 1998).

The effects of harvest on fungal persistence may show important regional variation in the Pacific Northwest. In dry, high elevation clearcuts of southwest Oregon, where temperature and moisture extremes pose severe stress, declines in mycorrhizal fungi have been noted (Amaranthus and Perry 1987). Similarly, studies in the northern Rocky Mountains have shown differences in fungal diversity between clearcut and undisturbed sites (Byrd et al. 2000). Hagerman et al. (1999), studying high elevation clearcuts in interior British Columbia, noted no initial differences between clearcuts and undisturbed sites, but recorded declines in fungal diversity two and three years after harvest. In contrast, cool coastal sites with greater organic matter and more equitable climate may be better able to maintain fungal populations through harvest cycles (Molina pers. com.). In addition, ectomycorrhizal fungal species show strong associations with specific tree or shrub species (Molina et al. 2001). It is currently unknown how fungal species diversity, biomass, and function are affected by conversions from mixed species assemblages to conifer plantations, but it is likely that species depending upon noncrop trees may be detrimentally affected. Hagerman, Sakakibara, and Durall (2000) demonstrated that retention of native understory shrub species may be important in maintaining diversity of ectomycorrhizal fungi morphotypes through harvest cycles. It should be mentioned that the few published studies of harvest effects on fungal communities have occurred in upland forests. Although many species and mechanisms overlap between upland and riparian forests, the unique conditions in riparian zones probably warrant further study.

Fungal communities are rich in species, and there are important successional relationships among taxa (Dix and Webster 1995; Molina et al. 2001). It is likely that most activities along the spectrum of timber harvest approaches will be beneficial to some taxa, but detrimental to others. However, as heterotrophic organisms, fungi require a carbon source and are typically most abundant and diverse where a variety of decaying wood substrates are readily available. Intact organic soils also provide habitat for many mycorrhizal species.

7.3.3 General Guidelines for Sustainable Forestry Practices

Forest management should aim to maintain diversity in stand species, structures, and ages and abundant, heterogeneous sources of large wood debris through space and time. Ground disturbing activities may be detrimental to fungal communities that require well-developed soils for establishment and growth. Flushes of successional vascular plant species (e.g., *Alnus*, *Ceanothus*, *Arctostaphylos* spp.) associated with disturbance may be important mycorrhizal host plants and essential for maintenance of diverse fungal populations at the stand and landscape scales (Hagerman, Sakakibara, and Durall 2000). Intensive shrub control practices may need to be relaxed following disturbances, to ensure that these seral species remain. Fungi require adequate moisture for growth and reproduction, so microclimatic changes associated with disturbance may pose considerable physiological stress in large disturbed areas, especially in more seasonal and droughty interior climates.

7.3.4 Information Needs

As organisms that exist primarily under the ground or in decaying wood, fungi are out of sight during most of the year. Basic information on the life history of fungi is needed for both upland and riparian ecosystems in the Pacific Northwest. Field inventories are needed, especially in remote areas, far from research universities. However, seasonal low-intensity inventories may be largely inaccurate and of limited utility for determining presence or absence of fungal species (Molina et al. 2001). The considerable time and taxonomic effort required to properly ascertain the status of fungal and lichen biodiversity argues for an ecosystem study approach, perhaps in concert with study of other small or cryptic organisms, such as bryophytes and forest invertebrates.

Great effort and expense have been expended to survey rare fungi on federal lands of the Pacific Northwest (Molina et al. 2001). A parallel effort of similar magnitude on private lands is not likely and may prove redundant. From the base of information being gathered under the Northwest Forest Plan, and targeted inventories on private lands, it may be possible to develop habitat models to determine distributions on private lands.

However, private lands may provide the best opportunity to evaluate the effects of multiple, relatively short rotation harvest, herbicide use, and perhaps other factors that are uncommon or absent on public land. In general, manipulative studies designed to determine relationships between harvest or disturbance intensity and fungal diversity and biomass are needed to determine harvest impacts and conservation strategies for managed landscapes. Such a research program might be replicated in a consistent way across landscape gradients to determine the interactions between landscape setting and harvest effects. Preliminary evidence indicates that heavy thinning (many trees removed) can substantially reduce mushroom productivity immediately after the harvest, but that lighter thinning (fewer trees removed) has a lesser impact on productivity (Pilz and Molina, unpublished data). The rate at which mushroom productivity rebounds as the remaining trees reoccupy a site has yet to be determined. Although it is likely that mixed stands will harbor greater diversity than stands of single species, it is unknown how quickly fungal species diversity might respond to disturbance or interplanting with native hardwood in otherwise conifer dominated stands (or vice versa). The recent finding that different tree species can translocate carbon below ground via fungal mycelium (Simard et al. 1997) may represent a functional relationship whereby species richness and ectomycorrhizae interact to maintain ecosystem integrity.

7.4 Mammals

Jennifer M. Weikel
Private Contractor
755 SE Summerfield Place
Corvallis, Oregon 97333

7.4.1 Introduction

Riparian forests in the Pacific Northwest are particularly important to mammals. Some 65% of the mammalian species occurring in Oregon and Washington use riparian areas and 27 species are threatened, endangered, or of special interest (Kauffman et al. 2001). Nine species are considered to be riparian obligates (Table 7.1). Many other species occur in both upland and riparian habitats, but are frequently more abundant (Doyle 1990; McComb, McGarigal, and Anthony 1993; West 2000a, 2000b) or have greater fitness (Doyle 1990) in riparian habitats (Table 7.2). In addition, because riparian forests are subject to relatively frequent disturbance, early succession-associated species of mammals are often more abundant in riparian forests than in upland habitats (Anthony et al. 2003). The degree of association with riparian areas often varies depending on geographic context, surrounding forest condition, and season (McComb, Chambers, and Newton 1993; Gomez and Anthony 1998; Kelsey and West 1998; Anthony et al. 2003). For example, whereas woodrats (*Neotoma* sp.) are not typically associated with riparian habitats throughout most of their range, they are associated with riparian areas in the more xeric forests of northwestern California and southern Oregon. In addition, generalist carnivores such as black bears (*Ursus americanus*), ringtails (*Bassariscus astutus*), and ermine (*Mustela erminea*) become more abundant in riparian areas in response to prey availability during spawning runs of salmon (Anthony et al. 2003).

Table 7.1 Riparian Obligate Species of Mammals in Coniferous Forests of Western Oregon and Washington (from Anthony et al. 2003)

Common Name	Scientific Name
northern water shrew	<i>Sorex palustris</i>
marsh shrew	<i>Sorex bendirii</i>
water vole	<i>Microtus richardsoni</i>
beaver	<i>Castor Canadensis</i>
muskrat	<i>Ondatra zibethicus</i>
nutria	<i>Myocastor coypus</i>
river otter	<i>Lutra Canadensis</i>
mink	<i>Mustela vison</i>
Columbia white-tailed deer	<i>Odocoileus virginianus leucurus</i>

The degree of association between riparian habitats and mammalian species depends, in part, on the size of the stream. Large-bodied highly aquatic mammals, such as river otters (*Lutra canadensis*), mink (*Mustela vison*), beaver (*Castor canadensis*), and riparian-associated mammals such as elk (*Cervus elaphus*) and deer (*Odocoileus* sp.), are most frequently associated with mid- to large-sized streams and rivers whereas most riparian-associated small mammals such as water voles (*Microtus richardsoni*) are associated with small sized streams (Kelsey and West 1998). In addition, riparian areas at low- to mid-elevations appear to be used more as travel corridors by some species than are riparian areas at high elevations (Kelsey and West 1998).

Table 7.2 Riparian-Associated Species of Mammals in Coniferous Forests of the Pacific Northwest (adapted from Anthony et al. 2003)

Common Name	Scientific Name	Notes
masked shrew	<i>Sorex cinereus</i>	early seral ^a
montane shrew	<i>Sorex monticolus</i>	
Pacific shrew	<i>Sorex pacificus</i>	
fog shrew	<i>Sorex sonomae</i>	
shrew mole	<i>Neurotrichus gibbsii</i>	
California myotis	<i>Myotis californicus</i>	
long-eared myotis	<i>Myotis evotis</i>	
little brown myotis	<i>Myotis lucifugus</i>	
fringed myotis	<i>Myotis thysanodes</i>	
long-legged myotis	<i>Myotis volans</i>	
Yuma myotis	<i>Myotis yumanensis</i>	
hoary bat	<i>Lasiurus cinereus</i>	
silver-haired bat	<i>Lasionycteris noctivagans</i>	
big brown bat	<i>Eptesicus fuscus</i>	
Townsend’s big-eared bat	<i>Corynorhinus townsendii</i>	
Allen’s chipmunk	<i>Tamias senex</i>	
bushy-tailed woodrat	<i>Neotoma cinera</i>	N. CA and S. Oregon ^b
dusky-footed woodrat	<i>Neotoma fuscipes</i>	N. CA and S. Oregon ^b

(Continued on next page. See notes at end of table.)

Table 7.2 Continued

Common Name	Scientific Name	Notes
white-footed vole	<i>Phenacomys albipes</i>	
long-tailed vole	<i>Microtus longicaudus</i>	
Oregon vole	<i>Microtus oregoni</i>	early seral ^a
western jumping mouse	<i>Zapus princeps</i>	early seral ^a
Pacific jumping mouse	<i>Zapus trinotatus</i>	early seral ^a
black bear	<i>Ursus americanus</i>	
raccoon	<i>Procyon lotor</i>	
ringtail	<i>Bassariscus astutus</i>	
American marten	<i>Martes americana</i>	
fisher	<i>Martes pennanti</i>	
ermine	<i>Martes erminea</i>	seasonal ^c
gray fox	<i>Urocyon cinereoargenteus</i>	
Roosevelt elk	<i>Cervus elaphus roosevelti</i>	seasonal ^c

^a Species is associated with early seral habitats, but is often more abundant in riparian areas due to frequent disturbances and thus early seral habitat characteristics in riparian areas.

^b Species appears to be associated with riparian habitats only in the drier regions of northern California and southern Oregon.

^c Species appears to be associated with riparian habitats seasonally.

The high degree of association between riparian habitats and mammalian species can be explained in part by riparian areas having predictable sources of water, abundant streamside insects, favorable microclimates, and high plant compositional and structural diversity (Kauffman et al. 2001; Anthony et al. 2003). Structural features that appear to enhance habitat value of riparian areas include large amounts of cover of deciduous shrubs and ferns, logs and woody debris piles, and snags (McComb, Chambers, and Newton 1993; Steel, Naiman, and West 1999; Hayes 2003).

Although bats are not typically considered riparian obligates, riparian areas are of particular importance to bats because they provide abundant insects for feeding and reliable sources of open water for drinking (Christy and West 1993; Waldien and Hayes 2001; Hayes 2003). The amount of use of any particular riparian area is dependent partly on the size and structure of the stream channel and the age or structural condition of both the riparian area and the surrounding forest. Bats forage more frequently over still water than over moving water and bats that forage close to water may avoid areas with surface clutter (e.g., rocks, woody debris) as well as sections of streams that generate a large amount of surface noise (Hayes 2003). In a study of bat use of intermittent streams in Douglas fir forests of northern California, Seidman and Zabel (2001) found that bat activity was greater over streams with channel widths > 1.8 m than over streams with channel widths < 1.2m or in upland areas. Relative to stand age and stand structure, bat activity tends to be greater in old growth than in young forests, and levels of bat activity appear to be negatively influenced by tree density (Grindal 1998; Humes, Hayes, and Collopy 1999; Erickson and West 2003; Hayes 2003). However, low levels of use by myotis bats and high levels of use by non-myotis bats of small clearcuts in western Oregon (Hayes and Adam 1996), suggests that the relationship between bat activity and tree density may be species-dependent and that for myotis bats, some intermediate density of trees may be optimal.

Mammals play an important role in actively shaping riparian habitats through activities such as selective herbivory, predation, burrowing, and trampling (Kelsey and West 1998; Kauffman et al. 2001). Mammals, especially carnivores that feed on salmon carcasses, play an important role in transferring nutrients from riparian to upland habitats (Anthony et al. 2003). Beavers are of particular importance. The beaver is considered a keystone species because it can dramatically alter riparian zones through selective herbivory and damming of creeks (Kauffman et al. 2001; Hayes and Hagar 2002). Their activities shape plant communities and the influence of many beavers within a single

basin can significantly change habitat and hydrological conditions (Kelsey and West 1998). Impoundment of water results in creation of ponds, retention of organic matter and sediment, death of trees, and creation of meadow habitat (Hayes and Hagar 2002). These features are in turn utilized by a variety of other wildlife species. Amphibians, fish, and aquatic birds utilize pond habitat, snags are used for nesting by cavity-nesting birds and for roosting by bats, and meadows are utilized by several small mammal and amphibian species (Suzuki 1992; Anthony et al. 2003). Beavers are not found in all riparian habitats, but instead prefer low gradient streams (< 3% gradient) in valleys about 25 to 30 m wide and with streams 3 to 4 m wide (Suzuki and McComb 1998).

Large ungulates such as elk and deer also have potential to influence riparian plant communities through selective herbivory. Ungulates tend to forage selectively on the most palatable hardwoods and conifers and in some cases heavy foraging can impede efforts in riparian restoration (Brookshire et al. 2002; Anthony et al. 2003). In addition, heavy use by ungulates can impact soil and affect stream channel structure (Kauffman et al. 2001; Anthony et al. 2003).

7.4.2 Ecological Processes and Habitat Features Related to Forestry Practices

Very few studies have examined the effects of timber harvest in riparian areas on mammals. Studies have been conducted on the effects of logging in riparian areas on bats in Oregon (Hayes and Adam 1996) and western Washington (West 2002b). Both studies found that activity levels of myotis bats were higher in wooded riparian areas than in adjacent clearcuts, whereas the reverse was true for non-myotis bats (mostly silver-haired bats [*Lasionycteris noctivagans*]). West (2002b) also found that level of bat activity did not differ between streams with wide (> 30m) and narrow (< 30m) buffers. This suggests that where myotis bats are negatively affected by clearcutting, retention of even narrow buffers should be beneficial.

West (2002a) studied the effects of logging in riparian areas on small mammals in western Washington. He determined that clearcut logging adjacent to riparian areas resulted in high species turnover and declines in abundance of forest-associated species of small mammals, including the marsh shrew (*Sorex bendirii*), Trowbridge's shrew (*Sorex trowbridgii*), shrew-mole (*Neurotrichus gibbsii*), and the forest deer mouse (*Peromyscus keeni*). However, retention of even narrow buffers appeared to be effective in maintaining many forest-associated species. Stream buffers appeared to provide habitat that was intermediate in quality between uncut control stands and clearcut uplands for forest-associated small mammals.

To my knowledge, no other studies in the Pacific Northwest have directly examined the effects of forestry in riparian areas on mammals. However, Anthony et al. (2003) have suggested that riparian buffers also may serve as refugia, but that to be effective for such a function, buffers would need to be large enough and to retain sufficient trees and shrubs to allow riparian-associated species to persist until sufficient tree canopy cover is reestablished in adjacent uplands. Riparian buffers likely will not be effective refugia for all mammal species, however, because some species are associated with upland forests (e.g., western red-backed vole [*Clethrionomys californicus*], McGarigal and McComb 1993; Hayes and Hagar 2002). Riparian buffers may also function as travel corridors. The role of riparian areas as travel corridors is well established for river otter, raccoons, black bears, bobcats, and deer (Anthony et al. 2003). The role of stream buffers to maintain function of riparian zones as travel corridors is not well studied, but has been documented for black-tailed deer (*Odocoileus hemionus columbianus*) in northern California (Loft, Menke, and Burton 1984) and for American marten (*Martes americana*) in Newfoundland (Forsey and Baggs 2001).

Watershed Scale Considerations. Only a few studies have assessed the role of landscape composition and configuration on mammals in the Pacific Northwest. In a study of associations of bats with local and landscape features in western Oregon and Washington, local stand structural conditions appeared to be more important than landscape features in influencing bat activity (Erickson and West 2003). In a study that examined patch and landscape level (sub-basin) habitat associations of small mammals in the Coast Range of Oregon, Martin and McComb (2002) found that red tree voles (*Arborimus longicaudus*), California red-backed voles (*Clethrionomys californicus*), and shrew moles were most frequently associated with unfragmented landscapes, deer mice (*Peromyscus maniculatus*) and white-footed voles (*Arborimus albipes*) were associated with fragmented landscapes, and marsh shrews, Pacific shrews (*Sorex pacificus*), fog shrews (*Sorex sonomae*), Trowbridges's shrews, vagrant shrews (*Sorex vagrans*), and Pacific jumping mice (*Zapus trinotatus*) were unaffected by landscape pattern. It appears that riparian-associated small mammals were associated more with local patch and microsite characteristics than landscape level patterns, with a possible exception of the shrew mole.

7.4.3 General Guidelines for Sustainable Forestry Practices

To ensure the maintenance of riparian-associated mammal communities within forested landscapes, retention of unharvested riparian buffers apparently is important when clearcutting adjacent to streams. Although current research suggests that even narrow buffers may be effective in retaining small mammal and bat communities in riparian areas, long-term studies of the effectiveness of riparian buffers are needed. Trees in riparian buffers, especially narrow ones, appear especially susceptible to blowdown (Bunnell, Kremsater, and Wind 1999; West 2000a, 2000b), and extensive windthrow of buffer trees reduces functionality of buffers (Kelsey and West 1998). Thus, whereas narrow buffers may be effective initially, wide buffers may be needed for long-term effectiveness. Bunnell, Kremsater, and Wind (1999) suggested that buffers dominated by hardwood trees may be more wind-firm than are buffers dominated by conifers. McComb, McGarigal, and Anthony (1993) suggested that buffers at least 50m wide would provide at least marginal habitat for the small mammal species that they studied. Kelsey and West (1998) suggest that buffers of 100–150 m wide will be needed to maintain preharvest microsite conditions.

Little information is available to inform guidelines to retaining mammalian biodiversity at large scales (e.g., watersheds). However, Martin and McComb (2002) suggest that landscapes that provide a full range of vegetation patterns (levels of fragmentation) and composition (variety of stand types and forest ages) will maximize species richness over large scales. Because some species of mammals are associated with upland habitats (e.g., red tree vole), use of only riparian buffers to provide travel corridors or late-seral forest refugia may not be effective to maintain biodiversity over landscapes managed for timber production (McComb, McGarigal, and Anthony 1993; Hayes and Hagar 2002).

Plantations bordering riparian areas may influence use of these areas by mammals. Plantations in the closed-canopy stem exclusion stage are structurally simple, are thought to host relatively few wildlife species, and no species is known to depend on this developmental stage (Hansen et al. 1991; McComb, Spies, and Emmingham 1993; Hayes et al. 1997). However, the value of even-aged plantations can be increased through retention of large-diameter trees, hardwood trees and shrubs, snags, and logs at time of harvest, and structural diversity can be increased through time by thinning (McComb, Spies, and Emmingham 1993; Carey and Curtis 1996; Hayes et al. 1997).

7.4.4 Information Needs

Although many studies have documented associations of mammals with riparian areas, information is still lacking on the influence of timber harvest on riparian obligate and associated mammals. To my knowledge, only one study has examined the role of riparian buffers on mammals in the Pacific Northwest (a multi-taxa study with effects on bats and small mammals reported in West 2000a, 2000b). Similar studies are needed elsewhere and may be especially pertinent in the more xeric areas

of the Pacific Northwest where the degree of association with riparian areas may be greater (Anthony et al. 2003).

Long-term studies are needed to examine effectiveness of buffers through time. To date, West (2000a, 2000b) has examined the influence of stream buffers only through two years post-harvest. It is possible that delayed influences of harvest may occur or that influences may decline over time as upland habitats become reforested. Long-term studies should also consider longevity of buffers, factors that influence windthrow, and implications of buffer longevity on the ability of buffers to continue to retain riparian- and closed canopy forest-associated wildlife communities in riparian areas.

Information is needed on the effects of partial harvest (e.g., commercial thinning, shelterwood harvest, individual tree selection) in riparian zones. To date, research on the influence of forest practices on wildlife in riparian zones in the Pacific Northwest has focused on effects of clearcutting and the influence of buffer width on bat and small mammal communities. Studies are needed on both a) influences of buffer width within the context of partial harvest in uplands, and b) the influence of partial harvest within both uplands and riparian zones (i.e., with no buffer). Both types of studies should explore varied levels of partial harvest (e.g., individual tree selection to commercial thinning or shelterwood harvest) and incorporate multiple taxa of mammals (e.g., carnivores, ungulates, bats, small mammals).

Current research has focused on effects of riparian zone management with regard to state forest practices rules (e.g., West 2000a, 2000b). There are currently no studies that compared prescriptions of state forest practices rules to those implemented under the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994). It has been suggested (e.g., Hayes and Hagar 2002) that continuous fixed-width buffers and use of only riparian buffers as refugia may not be effective or efficient approaches to maintaining biodiversity over large scales. Both observational and manipulative experiments are needed to address the relationship of various riparian management alternatives and response by wildlife. Kelsey and West (1998) suggest that maintaining islands of leave trees rather than continuous fixed-width buffers may be an effective approach to preserve microsite conditions and reduce risk of windthrow while also retaining both riparian and upland habitats. This approach is one alternative that could be studied and compared to various buffer retention strategies.

7.5 Birds

Jennifer M. Weikel
Private Contractor
755 SE Summerfield Place
Corvallis, Oregon 97333

7.5.1 Introduction

Riparian areas provide important habitat for bird communities in the Pacific Northwest. Although riparian zones make up only 1-2% of western landscapes, they provide breeding habitat for more species of birds than any other vegetation type (Kauffman et al. 2001). In Oregon and Washington, it is estimated that 266 species of birds occur in riparian habitats and that 103 of those species are closely associated with riparian habitats for breeding and foraging (Kauffman et al. 2001). In arid regions, a large proportion of bird species is more abundant or completely restricted to riparian areas (Knoph 1985). However, in wetter portions of the Pacific Northwest (Appendix A) where moisture is abundant due solely to high rainfall, fog, and high density of small streams, comparatively fewer bird species are dependent on riparian areas (McGarigal and McComb 1992). Nevertheless, riparian areas in the Pacific Northwest are often more structurally diverse and support more deciduous and berry-

producing shrubs, important food and nesting resources for birds, than do upland areas (Kelsey and West 1998; Lock and Naiman 1998). Riparian areas also frequently contain abundant large logs and woody debris piles which function as important structures for nest sites of winter wrens (*Troglodytes troglodytes*) (Waterhouse 1998) and as foraging and resting perches for many bird species (Steel, Naiman, and West 1999). Riparian habitats in the Pacific Northwest are particularly important for neotropical migrating birds; approximately 60-85% of neotropical migrating birds in the western United States breed in woody, deciduous riparian vegetation, and riparian areas are used more than are upland habitats by birds during migration (Kauffman et al. 2001). Riparian habitats also are important for raptors; roughly 50% of raptor species in western Oregon and Washington breed and 60% forage primarily in some type of riparian habitat (Knight 1988).

In the Pacific Northwest, composition of bird communities in riparian habitat is related in part to the size of the stream. Rivers and larger streams seem to be more important in providing habitat for riparian obligate bird species such as herons, ducks, and kingfishers than are smaller streams (Kelsey and West 1998; Hayes and Hagar 2002). In a comparison of bird communities between large and small rivers in western Washington, Lock and Naiman (1998) found that bird species richness and total abundance was higher in riparian areas of large rivers (active channel width 67-140m) than smaller rivers (active channel width 12-21 m). They also found that the ratio of deciduous to coniferous cover was a good predictor of bird species richness, which increased with deciduous cover, and that large rivers had a higher number of unique species not found in riparian habitats of the smaller rivers. Riparian habitat adjacent to large rivers appeared to be particularly important for raptors, neotropical migrants, and deciduous-associated species such as the black-throated gray warbler (*Dendroica nigrescens*) and warbling vireo (*Vireo gilvus*) (Lock and Naiman 1998).

Plant communities in riparian areas of small rivers and streams in western Oregon are typically similar to those in the adjacent uplands in moist coniferous forests (McGarigal and McComb 1992). Consequently, bird communities in riparian habitats of small streams are frequently similar to those found in adjacent upland habitats (McGarigal and McComb 1992; Lock and Naiman 1998). In a comparison of bird communities in riparian habitats around second and third order streams with adjacent uplands, McGarigal and McComb (1992) found that upland habitats actually supported higher bird species richness and total bird abundance than did riparian areas. They found that no species was unique to headwater riparian areas and only the Swainson's thrush (*Catharus ustulatus*) and winter wren were more abundant in riparian than in upland areas. In a similar comparison in western Washington, Pearson and Manuwal (2001) found that in addition to the winter wren, American robins (*Turdus migratorius*), black-throated gray warblers, and Pacific-slope flycatchers (*Empidonax difficilis*) also were more abundant in riparian than in upland areas.

Despite the fact that no bird species appears to be unique to riparian habitats of small rivers and streams in the Pacific Northwest, these habitats still provide vegetative structure and food resources important to birds. Small river and stream riparian areas typically support greater densities and cover of deciduous trees, deciduous shrubs, berry-producing shrubs, and herbaceous vegetation than do adjacent uplands.

7.5.2 Ecological Processes and Habitat Features Related to Forestry Practices

There is relatively little research on the relationships between timber harvest and birds in riparian areas of the Pacific Northwest, and thus far, research has focused on the function of riparian buffers to maintain pre-logging bird communities. In addition, research in the Pacific Northwest has been limited to examining buffers only along smaller rivers and streams.

Although no research has been conducted specifically on the influence of forestry on birds within riparian habitats of large rivers, there is some evidence suggesting that certain forest practices within this zone may negatively affect some species of birds. Nest sites of bald eagles (*Haliaeetus*

leucocephalus) in Oregon and Washington are often associated with mature coniferous forest within 2 km of large rivers (Garrett, Watson, and Anthony 1993; Buehler 2000). Productivity of bald eagles in Oregon was negatively correlated with proximity to clearcuts and major logging roads (Anthony and Isaacs 1989); however, territory occupancy and productivity were not negatively influenced by selective harvest in the Klamath Basin of Oregon (Arnett et al. 2001). In a study of habitat associations of riparian obligate bird species in the Coast Range of Oregon, Loegering and Anthony (1999) found a positive association between habitat use and the presence of forested cover (trees > 5 m tall) for American dippers (*Cinclus mexicanus*), belted kingfishers (*Ceryle torquata*), mallards (*Anas platyrhynchos*), and great-blue herons (*Ardea herodias*). Saab (1999) studied the influence of landscape pattern on birds in cottonwood riparian habitat with varying degrees of fragmentation in Idaho. She determined that bird species richness was positively associated with natural and heterogeneous landscapes, large patches of cottonwoods, close proximity to other patches of cottonwoods, and microhabitats with relatively open canopies.

Logging within riparian areas of small streams has a similar effect on bird communities as does logging in upland areas. Typically, logging within riparian areas results in a change in bird communities from dominance by species associated with closed-canopy coniferous forest to a community with greater representation of open-canopy or shrub associated species of birds (Hagar 1999; Pearson and Manuwal 2001). The extent of species turnover is related, in part, to retention of buffers. In a comparison of logged and unlogged riparian areas of the Coast Range of Oregon, Hagar (1999) found that unlogged riparian areas (>30 m buffer) retained bird communities dominated by closed-canopy forest-associated species (e.g., Hammond's [*Empidonax hammondi*] and Pacific-slope flycatchers, brown creepers [*Certhia americana*], chestnut-backed chickadees [*Poecile rufescens*], winter wrens, golden-crowned kinglets [*Regulus satrapa*]), whereas in logged sites, species associated with disturbed or open habitats (e.g., Rufous Hummingbird [*Selasphorus rufus*], northern flicker [*Colaptes auratus*], house wren [*Troglodytes aedon*], orange-crowned warbler [*Vermivora celata*], MacGillivray's warbler [*Oporornis tolmiei*], dark-eyed junco [*Junco hyemalis*], and American goldfinch [*Carduelis tristis*]) became more abundant and species associated with closed-canopy forests declined in abundance.

To my knowledge, no studies have been conducted on effects of partial cutting within riparian buffers or partial cutting that extends from the uplands and into the riparian zone (i.e., with no buffer). Hagar (1999), however, suggested that thinning or partial harvest of large-diameter trees within stream buffers might negatively affect species that are positively associated with tree density, such as Pacific-slope flycatchers and winter wrens.

Retention of unharvested buffer strips between streams and logged upland habitats is one approach that is often used to maintain biodiversity in riparian areas. Although buffer strips are often left for the goal of protecting habitat for fish and other aquatic vertebrates, they also provide habitat for many species of birds. Buffer width influences bird community composition. In western Washington and Oregon, buffers > 30 m wide retained similar bird communities compared to those present prior to harvest and in unlogged controls, whereas more narrow buffers (< 30 m wide) experienced higher species turnover (Hagar 1999; Pearson and Manuwal 2001). Even wide buffers, however, may not be adequate to support all species of birds (Kinley and Newhouse 1997, Hagar 1999, Pearson and Manuwal 2001). Interior-forest species, conifer forest species, and riparian-associated species appear to decrease in abundance even within buffers > 30 m (e.g., brown creeper, golden-crowned kinglet, black-throated gray warbler; Pearson and Manuwal 2001).

Watershed and landscape scale considerations. In addition, no studies have yet been conducted on the effects of riparian forestry at large scales such as watersheds. One study, however, suggests that landscape scale effects may occur. Saab (1999) studied the relative effects of microsite, stand-level, and landscape pattern on abundance of songbirds in cottonwood-dominated riparian areas of Idaho.

Within her study sites, riparian areas were fragmented primarily by agriculture. She found that landscape pattern (e.g., habitat patch size, shape, distance to other patches, fragmentation) was the primary influence on the distribution and that occurrence of most species and was more important than site specific or microsite characteristics. Although forest cutting is not common within hardwood-dominated riparian zones, the results of Saab (1999) suggest that where cutting does occur, it may be important to consider potential effects of landscape pattern as well as the cumulative effects from multiple land uses. Metrics are available for quantifying landscape patterns (e.g., FRAGSTATS, available at http://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html). See online documentation and McGarigal, Cushman, and Stafford (2000) for use of multivariate landscape metrics. Landscape metrics are commonly used to look at how patch size, fragmentation, etc. may affect wildlife.

7.5.3 General Guidelines for Sustainable Forestry Practices

More information is needed before comprehensive guidelines for sustainable forest management in riparian areas can be formulated. Because current research has been limited to use of riparian buffers, guidelines suggested here are restricted to use of riparian buffers along small streams (class 1-3). Within small stream riparian areas, current research suggests that buffers at least 30 m wide are needed to sustain pre-harvest bird communities (Hagar 1999; Pearson and Manuwal 2001). Thus, if sustaining pre-harvest bird communities is an objective, riparian buffers > 30 m wide should be left in some places to provide adequate habitat, especially for species associated with riparian habitats, such as Swainson's thrushes, black-throated gray warblers, and winter wrens. However, because bird communities within small stream riparian areas are similar to those found upland, smaller riparian buffers may sometimes be adequate, provided that sufficient forested habitat is provided in upland areas. In fact, given that more species of birds appear to be associated with upland than with riparian habitats (McGarigal and McComb 1992), it has been suggested that a combination of riparian management zones and upland stands with retained structure may be a useful strategy (Hayes and Hagar 2002).

Plantations in the closed-canopy stem exclusion stage are structurally simple and are thought to host relatively few bird species compared to more heterogeneous forests. No species is known to depend on this developmental stage (Hansen et al. 1991; McComb, Spies, and Emmingham 1993; Hayes et al. 1997). However, the value of even-aged plantations can be increased through retention of large-diameter trees, hardwood trees and shrubs, snags, and logs at time of harvest; structural diversity can be increased through time through thinning (McComb, Spies, and Emmingham 1993; Carey and Curtis 1996; Hayes et al. 1997).

7.5.4 Information Needs

Relatively little is understood about the effects of forestry within riparian zones on birds. Most research has focused on the role of riparian buffers to conserve pre-logging bird communities in headwater streams. There appear to be four major information gaps with regard to the influence of forest practices in riparian zones on birds. First, research is needed to determine potential impacts of forestry on birds in riparian areas of large streams and rivers (stream class 3 and above). As noted above, most riparian obligate and many riparian associated species of birds are associated with the open water and riparian habitat of large streams and rivers; however, little is known regarding the potential influence of forest practices on these species.

Second, information is needed on the effects of partial harvest (e.g., commercial thinning, shelterwood harvest, individual tree selection) in riparian zones. Research on the influence of forest practices on wildlife in riparian zones has focused on effects of clearcutting and the influence of buffer width. With the exception of Arnett et al. (2001), no information has been published on the influence of partial harvest on riparian-associated wildlife. It is likely that partial harvest in both

riparian and upland habitats will have less influence on microclimate and habitat within riparian zones than does clearcutting and that these differences would be reflected by responses of bird species. Studies in upland habitats suggest that commercial thinning does not have a dramatic negative effect on bird abundance (e.g., Hagar, McComb, and Emmingham 1996; Hayes, Weikel, and Huso 2003). However, of the species that were negatively affected by thinning, some are generally considered to be riparian-associated species (e.g., Pacific-slope flycatcher and black-throated gray warbler). Thus, partial harvest both in uplands and in riparian zones may have larger implications for some species' sustainability. Studies are needed on both a) influences of buffer width within the context of partial harvest in uplands, and b) the influence of partial harvest within both uplands and riparian zones (i.e., with no buffer). Both types of studies should explore varied levels of partial harvest (e.g., individual tree selection to commercial thinning or shelterwood harvest).

Thirdly, information about the ability of riparian buffers to conserve bird populations over the long term is needed. Although research has shown that wide buffers can be used retain pre-logging bird communities, no research has yet been conducted on whether buffers are effective in conserving these species as adjacent forests regrow over the long term or whether reproductive productivity of birds within buffers is affected. The positive association of Steller's jays (*Cyanocitta stelleri*), a known predator of bird nests, with riparian buffers in Oregon (Hagar 1999), suggests that nest depredation within buffers may be a concern. Pearson and Manuwal (2001) and Hagar (1999) have indicated that research is needed on nest depredation and productivity of birds within riparian buffers. Research is also needed on population viability of species that decrease in abundance with decreasing buffer width.

Lastly, current research has focused on effects of riparian zone management with regard to state forest practices rules (e.g., Hagar 1999; Pearson and Manuwal 2001). There are currently no studies that compare prescriptions of state forest practices rules to those implemented under the Northwest Forest Plan (USDA Forest Service and USDI Bureau of Land Management 1994). Both observational and manipulative experiments are needed to address the relationship of various riparian management alternatives and response by birds.

7.6 Invertebrates

Andrew R. Moldenke
Department of Entomology, Oregon State University
Corvallis, Oregon 97331

7.6.1 Introduction

Animals without backbones comprise most of what has been termed "the hidden 99.5%" of life's diversity, and have been described as the "little things that run the world" (Wilson 1987). Not surprisingly, invertebrate life forms are important parts of the biodiversity spectrum that greatly influence the productivity and function of forests (Marcot 1997; Showalter et al. 1997). This section will focus on Arthropods (i.e., the Phylum that contains insects, arachnids, and crustaceans), which are by far the most diverse group in any forest landscape (Showalter et al. 1997). In fact, there are many times more species of native arthropods than all the vertebrates, higher plants and macro-fungi combined. Although the present treatment does not discuss all invertebrate life forms, it does not imply that often overlooked invertebrates are not important elements of biodiversity. For example, Frest (2002) recently described the importance of native snails as indicators of ecosystem health. Many mollusk species are local endemics (Marcot 1997); presumably a large number of flightless arthropods are likewise endemic (e.g., amaurobiid spiders, *Melanopus* grasshoppers, caseyid millipedes).

Because of the vast number of taxa and life history variations, the invertebrate discussion here will be general, but sources of more specific information are provided.

Invertebrates inhabit all environments from the mineral regolith underlying riparian forests to the upper reaches of the canopy and beyond. Although relatively large herbivores and predators are the most conspicuous invertebrates in any forest, the more inconspicuous detritivore group is the richest in species. As a general rule, the “soil” is the most diverse component of the riparian ecosystem, hence the focus here. There are probably in excess of 10,000 species of arthropods within the region. Most of these arthropods are intimately associated with the soil/litter for at least part of their life cycles. Most are found in both riparian and upslope habitats, but there are differences as described below.

No comprehensive listing exists of these species, nor is there any systematic compilation of the relevant literature (Moldenke and Ver Linden 2002). For an ongoing literature review and database development project on Pacific Northwest Arthropods, Moldenke and Ver Linden have searched the databases (tens of thousands of references) for major taxonomic groups: spiders (Araneae), turtlemites (Oribatida), carabid ground-beetles (Carabidae), longhorned-beetles (Cerambycidae), bark-beetles (Scolytidae), flies (Diptera), springtails (Collembola), bees (Apoidea). Additionally, they searched the database for inventory techniques and soil ecological terms in order to compile an annotated bibliography of the most pertinent references (most recent continually updated version subsequent to this one may be found at <http://www.ent.orst.edu/moldenka>). Although this database does not focus strictly on riparian species, it does serve as a valuable source of information about arthropods in riparian areas.

Despite gaps in knowledge, it is clear that mesic forests west of the Cascade Crest, from which fire has been excluded, have very deep litter layers and quite probably support the highest densities and diversities of soil arthropods anywhere in the world (Moldenke 1999). Though the relative arthropod biomass cornucopia of the stream habitat versus the upland has been documented in desert environments, it seldom has been quantified in temperate forest habitats. However, it is likely that the same phenomenon occurs in the Pacific Northwest conifer biome. Studies by Brenner (2000) and Moldenke (in prep) in the past decade have shown that both the diversity and the abundance of large terrestrial arthropods increases dramatically as one approaches a stream.

These higher densities are comprised of two distinct types of species: a) those restricted in all of their activities to the terrestrial-riparian zone; and b) those typical of the upland but which visit the riparian zone presumably in search of both more abundant food and available drinking water. There is probably a far higher level of available arthropod biomass in the ground-surface stratum than in either the foliage-gleaning or the fly-catching strata. It is known that the arthropod species inhabiting this zone are active at distinct times of the year, and that species richness of arthropods is extraordinarily high. In fact, the Moldenke and Joseph Furnish studies (unpublished) have shown that terrestrial-riparian zones are twice as species rich as upland forest floor areas, and that nearly 100% of the true forest floor species occur within the terrestrial-riparian zone (>75% of them are actually more abundant within the terrestrial-riparian zone). Microclimatic heterogeneity plus habitat diversity created by the unpredictability of streamflow events (as well as an abundance of food resources) causes the significantly enriched biodiversity in the streamside environment (Antvogel and Bonn 2001; Collinge et al. 2001).

Arthropods are of particular significance to all biodiversity as well for a multitude of reasons. Perhaps most critical are:

- 1) They play an important role in the development of soil organic matter as regulators of microbial growth, nutrient decomposition and plant growth. The long-term health of any ecosystem is intimately dependent upon minimizing the rate of nutrient loss: the greater the biomass of soil

microbes, the slower the rate of nutrient loss. The progressive decrease in soil organic matter (both living and dead) in agricultural soils in North America is a major factor leading to chemical pollution in waterways and aquifers. Soil degradation is associated with a decrease in soil fauna diversity (Coleman and Crossley 1996; Benckiser 1997).

- 2) They are a major food source for vertebrates and are therefore vital to trophic transfer. Insects on the wing are the prime food resource of fly-catching birds and bats. In large regions of the forested Northwest, both the abundance of shrubs and caterpillar biomass increase as one approaches a stream channel (Jiquan Chen, Department of Environmental Sciences, Michigan Technical University, unpublished data). There is a greater diversity of vertebrates utilizing the terrestrial ground-surface arthropod food resource than either the foliage or aerial environments.
- 3) They provide trophic sustainability through pollination. Pollination services are often taken for granted. It is often assumed that plants are being efficiently pollinated. However, many environments are pollinator-limited—even within environments richly characterized by pollinators, a large percentage of species lose out in competition to species with big showy flowers (Moldenke 1975, 1976a, 1979b, 1979c). Pollinator services are thus of concern in all environments. The vegetation zones of the Pacific Northwest have rarely been characterized with respect to their pollinator abundances and behaviors, unlike those in California (see Moldenke 1975, 1976a, 1979a). Marcot et al. (1998) estimated that in the interior Columbia River Basin, invertebrates pollinate most of the rare or potentially rare vascular plants (66%), and about half of these plants (33%) are pollinated by solitary bees (Rathcke and Jules 1993; Bond 1994; Haynes, Graham, and Quigley 1996; Spira 2001). In this region, insects as a whole play vital roles in reproduction of rare flowering plants, whose viability depends on the presence of their invertebrate pollinators and dispersal mutualists.
- 4) They function as disturbance agents. Bark beetles and associated fungi are often critical in the formation of forest gaps through tree mortality, increasing habitat heterogeneity, and allowing light to reach the forest floor. This creates opportunities for a different suite of herbs and shrubs in the understory. The downed trees become decomposing logs, which provide for numerous species, not only of arthropods and fungi, but nitrogen-fixing bacteria, etc. Trees killed by insect/pathogen interactions may also facilitate fire occurrence and promote heterogeneity in fire effects (Agee 1993).

7.6.2 Ecological Processes and Habitat Features Related to Forestry Practices

Two general management practices will have the most significant and farthest-reaching effects in Pacific Northwest forestry: timber removal and prescribed fire (including both broadcast and pile burning of slash). Regardless of the logical and pertinent arguments that compare these processes to natural disturbance events, it is recognized that many aspects of both are not similar to natural disturbances. *A priori* we know that forest management practices all have strong effects, either directly on species (e.g., effects of heavy machinery on soil organisms) or indirectly through initiating successional changes (i.e., there are open-canopy taxa and closed-canopy taxa) and associated changes in microclimate, litter depth, or habitat heterogeneity. Ongoing studies by Niwa and Rappaport (unpublished) are an excellent start to understanding the role of controlled underburning on soil macro- and micro-fauna. Niwa's studies have revealed either no detectable effect on most individual species and functional groups area-wide of either spring or fall underburning or small quantitative effects which rapidly return to pre-burn conditions, in contrast to Miller and Moldenke's previous studies which showed legacies lasting 35+ years from "hot" site-prep burns (Estrada-Venegas 1995). It may also be instructive to compare results from these studies with results from similar studies in other regions (e.g., Kalisz and Powell 2000; Wikars and Schimmel 2001),

particularly regarding influence of management practices on arthropod functional groups and ecological roles.

The structural and microclimatic changes resulting from logging disturbance have differing implications for arthropod diversity that are strongly dependent upon the habitat needs of a specific species group. For example, for some flying arthropods which depend upon sunlight for warming of flight muscles (e.g., butterflies), the increased insolation associated with disturbances may be favorable (Meyer and Sisk 2001). Yet other species may be negatively affected by the same disturbance if they are dependent upon undisturbed soil, tree boles, or downed wood for food or habitat.

Forestry practices will affect both the community of soil arthropods and the soil processes in which they participate in direct proportion to the intensity of the disturbances. In forest environments the litter layer is apparently positively correlated with arthropod density and diversity in most cases (Madson 1997). Forestry practices (such as clearcutting, underburning, and fuel removal) may initially decrease total density of soil-dwelling arthropods by 75-90% and decrease species richness by more than 50% (Moldenke et al. unpublished data). Deep soil compaction (through mechanized vehicle use and log skidding) is probably the most radical change in any environment to soil arthropods. The ability of species to recover from such impacts is not known.

Does protection of riparian buffers actually protect the entire forest floor fauna? The actual functionality of riparian buffer widths for maintaining diversity and population densities of both aquatic and terrestrial-riparian arthropods needs to be assessed in both the mesic forests of the Northwest and the more xeric forests of the eastern Klamath region and the east side of the Cascades (see research of Rykken and Moldenke, unpublished). Studies by Chan and Olson and others (Olson et al. 2000a, 2000b, 2000c; Tappeiner, Olson, and Thompson 2000; Rundio and Olson 2001) have shown that the diversity of terrestrial-riparian microhabitats is positively related to increased frequency and amplitude of natural disturbance. Future management of riparian zones needs to focus on appropriate levels of habitat disturbance and overall effects (i.e., habitat heterogeneity, legacy retention, and physiological stress) within the riparian zone on arthropod diversity. Literature reveals that in Europe and eastern North America, the terrestrial-riparian fauna varies by stream order, canopy cover, and disturbance regime (Erwin, Ball, and Whitehead 1979; Desender 1994).

Intensive forestry has been shown to affect both the diversity and functional role of soil arthropods. Springett (1976) compared the diversity and abundance of soil arthropods and litter decomposition in natural woodlands and pine plantations. Although there was no clear relationship found between arthropod abundance and decomposition, there was a significant correlation between species diversity and decomposition rates. Notably, there was a large effect at low diversity values, and a decreasing effect at more usual levels of diversity. This has been taken as evidence that a certain minimum number of species may be required for full ecosystem function (Davis et al. 1996), which supports theoretical models relating diversity and functioning of ecological processes (Vitousek and Hooper 1993).

7.6.3 *General Guidelines for Sustainable Forestry Practices*

Any management practices that tend to decrease stream heterogeneity are likely to alter arthropod diversity. The microhabitat associations of riparian arthropod species still need to be documented especially as they relate to stream width and lateral distribution of species into the upland forest floor (current unpublished research by Moldenke, Chan, and Olson). It must be emphasized that the richness of riparian-associated terrestrial species far exceeds the richness of true aquatic species.

There are sensitive arthropod species, assemblages, or communities that appear excluded from present management set-asides that should be considered. Most species that are “sensitive” to soil

disturbances in unprotected natural sites are probably restricted to areas without a forest canopy. However, there still exists the question of what sensitive taxa might be restricted to forested habitats with commercial potential (the cryptic-sensitives); hence the need to inventory and sample in a statistically rigorous fashion. Riparian areas are the most likely areas to support habitat-restricted arthropod taxa, regardless of canopy cover. Ancillary wetland habitats (i.e., bogs, marshes, etc.) perhaps sustain even higher species richness and endemism of terrestrial arthropods (e.g., the majority of species of ground-beetles [Carabidae and Staphylinidae] are associated with microenvironments that are basically “riparian”) and need appropriate attention in practical measures to protect riparian biodiversity as well (Lindroth 1961-69; Thiele 1977; Stork 1990; J. Richardson, Dept. Entomology, University of British Columbia, Vancouver, BC., in prep.).

Having a regional forest conservation program in place does not necessarily mean that very localized endemic species and subspecies will be protected. Historically, the elevated biodiversity of arthropods has functioned to hinder community-wide faunal analyses. Current development of computer imaging algorithms is at the point when the entire aquatic insect community of the region will be recognizable at the level of species, once a data file of appropriate pictures can be assembled.

7.6.4 Information Needs

A substantial percentage of the forest land base is/will be tied up in riparian buffers. How wide must buffers be to protect aquatic and terrestrial-riparian invertebrates? How do requirements of these individual species differ between headwater/first order, third order, and fifth order/rivers and streams? More studies like those conducted in central Oregon by Furnish/Progar/Moldenke (Progar and Moldenke 2002) need to be initiated. These have documented that: a) temporary headwater streams produce higher densities of invertebrates (i.e., migratory bird food) than continuous-flow primary streams; b) continuous-flow primary streams have higher levels of diversity/species richness than temporary ones; and c) the unique species in the temporary streams are not true aquatic species, but are related to terrestrial-riparian species—whether they are unique or widespread in terrestrial habitats is unknown.

If biodiversity-linked assays are critical anywhere within the forested Pacific Northwest, then they must be critical in the Klamath region. Studies on soil arthropods conducted elsewhere (e.g., Postle, Majer, and Bell 1991; Deharveng 1996; Pankhurst, Doube, and Gupta 1997; Neher et al. 1998; Bird, Coulson, and Crossley 2000; Haskell 2000) may not necessarily directly pertain to conditions in the Klamath region. Quaternary history has seen alternating northward and southward migration of thousands of arthropod taxa associated with the glacial cycles. Throughout this long and heterogeneous geological period, the Klamath region has served as refuge for both Arcto-Tertiary (Temperate) and Madro-Tertiary (Tropical) fauna. Additionally, the region’s edaphic heterogeneity has served as a focus for neoendemic radiation of species (e.g., *Malanopus* grasshoppers).

8.0 KEYSTONE AND ENDANGERED SPECIES

8.1 Keystone Species and Related Concepts

In this section, we discuss the concept of keystone species and related topics of keystone processes and habitat features. Specific effects of keystone species such as beavers and ungulates on vegetation are described in Section 7.1, and on wildlife habitat in Section 7.4. Keystone concepts are also described for insect assemblages in Section 7.6.

Specific management for all elements of biodiversity is impossible. This logistic reality has led to great interest in keystone species or endangered species as surrogates for biodiversity as a whole. In concept, keystone species are those whose removal would cause a disproportionate alteration of a critical biological process, and presumably, loss of biodiversity. In many cases, these species are required to maintain a trophic balance, such as top predators that exert controls on herbivore populations which in turn, govern vegetation structure and composition of entire ecosystems (Perry 1994; Thompson and Angelstam 1999). Examples of such top predators include wolves, which control moose, which exert secondary effects on vegetation and soils on Isle Royale in Lake Superior (Brandner, Peterson, and Risenhoover 1990), and sea otters, which prey on sea urchins, and allow persistence of kelp forests along the Pacific Coast (Estes and Palmisano 1974). Other species, such as beavers or earthworms, that function as ecosystem engineers are also considered keystone species (see Sections 7.4 and 7.6). Beyond these apparently clear examples (e.g., there is much more to Isle Royale plant/animal dynamics than interactions between moose and wolves), there may be many other species that play disproportionate roles in maintaining biodiversity, through their effects on nutrient capture (e.g., nitrogen fixation in *Alnus*, *Ceanothus* spp.), large wood development (Douglas fir, Port Orford cedar, redwood and other large conifers), or water and nutrient capture by plants (various mycorrhizal fungi species). More recently, the keystone concept has been expanded to include keystone ecosystems (e.g., riparian forests, aspen groves, wetlands), or processes (e.g., fire, flooding dynamics) as landscape factors associated with high biodiversity (Perry 1994; Stohlgren et al. 1997). In other cases, the impacts from introductions of non-native species can be so great that they act as artificial keystones (e.g., Port Orford cedar root rot (*Phytophthora lateralis*); giant reed (*Arundo donax*) in riparian forests of California).

The premise that single species or small groups of species function as strong controls on ecosystems is controversial, and related to scientific discussions of the role of species diversity on ecosystem stability (e.g., Elton 1958; Tilman 1996). Clearly, most species perform roles that are both distinctive and to some degree redundant, whereas some others are of more singular importance. Quite aside from the problematic ethical assertion that any species has more value than another, management for only the most distinctive species may be an incomplete approach, because native ecosystems should have a degree of species redundancy in most functional roles (Tilman 1996). However, identification of potentially important species or processes that are absent or impaired may be one of the most effective starting points for restoring the biodiversity potential of a degraded riparian forest.

Although it is clear that the keystone species concept encompasses a very important and practical topic, most descriptions of keystone species are anecdotal, and probably clouded by our unbalanced knowledge of and affection for individual species. Although few would argue that charismatic species such as wolves or beavers play essential roles in ecosystems where they occur, there is little way of evaluating whether these roles are more essential than, say, those of seed caching-rodents, nitrogen-fixing bacteria, or certain species of soil arthropods. In some cases, manipulative studies have clearly demonstrated the importance of single species for biodiversity. A classic example is the study that demonstrated the role of the food-web keystone, the starfish *Pisaster*. It was only discovered to have a key role in regulating the abundance of other species in Pacific Northwest intertidal communities

when it was experimentally removed. Removal caused a drastic shift in dominance, and species richness fell from 15 to 8 (Paine 1980). Such experimental approaches are illustrative, but it would both be logistically impossible and ethically untenable to advocate such species removal experiments to be applied more broadly in riparian forests of the Pacific Northwest. However, the unregulated trapping, livestock grazing, logging, and hydrologic alterations of the 1800s and early 1900s may have already removed many species, structures, or processes from riparian forests of the region, establishing, in effect, unintentional experiments.

In riparian forests in the Pacific Northwest, several factors may be sufficiently impaired to be limiting biodiversity. Past trapping of beavers and loss of associated wetland complexes may have resulted in significantly reduced biodiversity in managed forests as compared to historic levels, essentially by reducing habitat heterogeneity. Similarly, removal of large conifers and large woody debris from streamside forest, or the active channel in the case of Port Orford cedar, may have caused substantial changes in the habitat quality of streams and floodplains, with important implications for many elements of biodiversity. In drier locales, fire may represent a keystone process that has been affected, with unknown effects on biodiversity. Introduced plant or animal species such as tree of heaven (*Ailanthus altissima*) and the brown-headed cowbird (*Molothris ater*) may presently be exerting strong influences on the biodiversity of riparian forests in parts of the region. In each of these examples, restoration of the impaired species or processes, or removal of the introduced species, may be valuable for increasing or maintaining riparian biodiversity.

Restoration ecology may provide a platform for manipulative research evaluating “keystoneness” that is both scientifically and ethically desirable. Carefully designed experiments that restore certain keystone elements (e.g., beaver, large wood, fire) and measure responses in riparian biodiversity may provide a means to test hypotheses about keystone function as well as mechanisms of ecosystem recovery.

8.2 Rare, Sensitive, and Endangered Species

Although an integrated view of biodiversity would encompass a vast array of species and processes in any landscape, rare, sensitive, and endangered species draw disproportionate attention because they are especially imperiled, are charismatic or otherwise well known, and they are protected by law. It is beyond the scope of this problem analysis to speculate on whether society should allocate special status to endangered or threatened species. That has been dealt with authoritatively in appropriate forums (USDA and USDI 1994). None of the concepts in this problem analysis challenge existing policy with regard to rare or endangered species. We support the general premise that especially vulnerable species warrant greater attention from researchers and managers, yet we aim this document toward articulation of principles for maintaining habitat for diverse species assemblages in riparian forests.

Rarity is an important characteristic of certain elements of biodiversity that may or may not intersect with forest management. As with most species occurring in riparian forests, rare species can be affected by the changes in forest structure and composition associated with forestry practices. However, they merit special consideration because for species with very restricted distributions, entire populations may be easily extirpated by forest disturbances (Thompson and Angelstam 1999). Strict preservation may also be detrimental if the species in question are associated with specific seral states or otherwise dependent upon disturbance. Managers, therefore, should seek information not only on the locations of rare species populations, but the actual structural or microhabitat requirements that the species require through time.

Sensitive species may perform an important role as indicators of subtle habitat changes associated with management. Amphibians, for example, may be among the most sensitive taxa in riparian forests of the Pacific Northwest, and may illustrate the biological significance of management changes more

effectively than other prominent organisms, such as vascular plants. As Sections 6 and 7 illustrate, species differ strongly in sensitivity to similar silvicultural treatments. Sensitive species may require special consideration when planning activities in riparian forests. If management takes a completely protective approach, however, other elements of biodiversity may be detrimentally affected. Viewed at a landscape perspective, relatively stable, low stress environments and disturbed environments are probably both required for maintenance of overall biodiversity.

As mentioned above, the methods for establishing categories of extinction risk developed nationally and internationally are detailed and exhaustive (Thompson and Angelstom 1999), and exceed the scope of this document. Impacts to individual rare species and/or related ones for which applicable information exists are described in Sections 6 and 7. The general approach in recovery plans for such species is to identify and protect habitat areas considered particularly important and to manage these with an overriding goal of fostering the species recovery as illustrated by the FEMAT process (USDA and USDI 1994). It is clear from examination of the lists of threatened and endangered species, that the species most likely to find critical habitat in riparian forests or the Pacific Northwest are fish, particularly anadromous salmonids.

We refer the reader to the following websites for further reading about threatened and endangered species in the Pacific Northwest.

Federally protected threatened and endangered species in the Pacific Northwest are listed by the U.S. Forest Service's Pacific Northwest Research Station at <http://www.fs.fed.us/r6/nr/wildlife/tes/list/index.htm>.

Lists of threatened and endangered species recognized by the state of California are at http://www.dfg.ca.gov/hcpb/species/t_e_spp/tespp.shtml; those recognized by Oregon at http://oregonstate.edu/ornhic/2004_t&e_book.pdf; and those recognized by Washington at <http://wdfw.wa.gov/wlm/diversty/soc/concern.htm>.

PART III APPROACHES FOR PROTECTING RIPARIAN BIODIVERSITY

9.0 SYNTHESIS AND SUMMARY OF TAXA-SPECIFIC RESPONSES

Silviculture, timber harvest, yarding, and transportation infrastructure, through their effects on legacy retention, physiological stress, and related resource availability, can affect riparian biodiversity. How these factors affect biodiversity can vary considerably with the taxonomic group as described in detail in Sections 6 and 7. We synthesize this detailed information here.

9.1 Effects on Aquatic Biodiversity

Forestry practices, including roading, have been linked to declines in diversity of fish populations in the Pacific Northwest (Section 6.1). Primary explanations are poor egg and juvenile survival because of increased temperatures, frequent fine sediment input, and reduced legacies, primarily large woody debris in streams. Large woody debris provides energy and nutrients for fish production via decomposition processes; it also provides sediment-trapping value. Effects are complicated however, with important regional variation. In relatively cool, maritime climates west of the Cascades, dense tall conifer canopies may limit within-stream photosynthesis; as a result, invertebrate and fish productivity often increase in streams with removal of canopy vegetation. Whether this translates to competitive dominance is unclear. In drier southern or interior climates, sharp temperature rises are often noted with canopy loss. The net effects of logging practices on solar radiation, sedimentation, and hydrology appear to have important regional variation. In contrast, removal of sources of large woody debris leads to degraded conditions for spawning and rearing of salmonids in most

environments. These same processes affect habitat quality for stream-dwelling amphibians to varying degrees depending on species' life history attributes and behaviors and the geomorphic stability of the stream channel (Section 6.2). Stream amphibians appear to be among organisms most sensitive to the effects of timber harvest in most climatic settings. For aquatic invertebrates (Section 6.3), community composition changes with alteration of physical factors such as fine sediment concentration and organic inputs, including woody debris. Biomass of some grazing aquatic invertebrates may increase with increasing solar radiation and consequent rises in within-stream photosynthesis, whereas removal of streamside vegetation can ultimately be detrimental to animals such as detritivores dependent on the supply of organic matter provided by streamside plants.

9.2 Effects on Terrestrial Biodiversity

Effects of timber harvest on terrestrial species that occupy riparian areas for most or all of their life cycles also show considerable variation by life form, type of harvest, and location. For vascular plants, the direct effects on merchantable tree species depend on harvest and regeneration dynamics in a particular location. Effects on other species will depend on soil disturbance and physical damage incurred during harvest and yarding. Intensity of disturbance effects and legacy retention will have important influences, as will related, widely varied rates of recovery. In addition, the changes in physiological stresses and growth resources associated with disturbance will vary geographically. Following harvests, composition shifts to fewer shade-tolerant species and an increase in ruderal and non-native species (Section 7.1). Depending on legacy retention, physiological stress, and non-native species, recovery of biodiversity may be hindered.

Non-vascular plants (Section 7.2) generally are more shade-tolerant and less tolerant of heat than most vascular plants. Consequently, they are often more sensitive to removal of shade-casting vegetation. Moreover, tree boles and downed wood serve as substrata to these species, so they are affected by both physiological stress and resource availability following timber harvest. Fungi are species rich, with many forms occurring in all successional stages of native forests (Section 7.3). However, as heterotrophs, fungal species are strongly dependent on specific carbon sources in the form of woody debris, soil organic layers, or mycorrhizal host plants of a variety of species. Where forest management removes or changes these carbon sources, fungal biodiversity can be affected.

The responses of terrestrial wildlife to silvicultural activities in riparian areas are often uncertain and complicated (Sections 7.4 and 7.5). Many species use riparian areas to varying degrees. Both riparian conditions and those of adjacent uplands will be important. Riparian areas along large streams are especially important to birds. A number of wildlife species may be keystones, with beavers being the most obvious. They enhance local and landscape scale diversity. Effects of forestry practices on terrestrial arthropod communities are more predictable and generally more detrimental than to other animals as the diversity and abundance of these species tend to be directly proportional to amounts of litter, soil organic matter, and understory deciduous species (Section 7.6). The extent to which arthropods are affected will depend again on yarding and other factors affecting soil disturbance. Other species of arthropods are directly affected where timber harvest or understory management removes host species.

Effects of forestry disturbances on habitat heterogeneity and quality, physiological stress, and resource availability show considerable variation across taxa groups and landscape settings. Variations in stress tolerance or requirements for resources among life history groups illustrate clearly that no single species or group approach will be most beneficial for all taxa. Moreover, because species groups show differential sensitivity to forestry practices, it will be difficult to assess overall impacts of treatments. Although an evaluation of the effects of any management activity must ultimately include a consideration of life history requirements, these data are not available for most taxa. Further, the relative influences of resource availability and physiological stress will also vary

geographically (Figures 4.2 and 4.3). For example, in the drier, more variable climate of the eastern Cascades and Siskiyou, open, disturbed environments are expected to pose relatively greater physiological stress for a given disturbance intensity, frequency or size.

Despite the uncertainty and variation, it may be possible to manage so as to emphasize protection of target taxa that are most sensitive to logging disturbance in a given region. These will be species for which conditions with respect to both resource needs and physiological stress are detrimental. Amphibians, non-vascular plants and soil arthropods are very sensitive taxa because essential resources (i.e., habitat, food) are removed and supportive environmental conditions are changed by timber harvest. Moderately sensitive taxa, such as ectomycorrhizal fungi or stream fauna, may be only lightly affected by harvest in the coastal mountains but may be detrimentally affected by harvest in somewhat more severe climates, such as the Klamath region (Molina pers. com.). Still other groups, such as vascular plants and birds, may show greater sensitivity to riparian harvest east of the Cascades.

Considering these factors, along with habitat heterogeneity and quality, broader conclusions exist as well. Riparian forests with varied tree species and age classes, occasional shrub-dominated patches, and woody legacies such as snags and downed logs, have high potential to maintain biodiversity, whereas even-aged, single-species stands often lack the legacies and heterogeneity that underlie biodiversity. Of particular interest to forest managers wishing to restore biodiversity is the proportion of heterogeneity that can be manipulated by forest managers at the stand scale. Other, less changeable characteristics such as geomorphology or geological diversity may be most useful in helping to characterize areas with high potential for diversity. *A better understanding of effective habitat heterogeneity for different life history groups may be one of the greatest information needs for biodiversity conservation in riparian forests.*

10.0 STAND-SCALE APPROACHES FOR PROTECTING BIODIVERSITY

Species habitat is strongly governed by availability of limiting resources such as energy and nutrients, which are influenced by such things as organic inputs in streams, the vertical and horizontal arrangement of vegetation, logs, and snags, and associated variation in plant species composition. All of these factors can be strongly influenced by stand-level silvicultural practices.

Stand-scale approaches for improving biodiversity maintenance should be effective where physiological stress can be reduced and where habitat heterogeneity, and legacy and limited resource retention can be improved. Even at the stand scale, an ecosystem perspective is needed to evaluate potential management adjustments, and determine their overall effects (Gregory 1997). Stand starting conditions and potential, as well as site-specific factors will likely weigh heavily in analyses of what treatments are effective, feasible and worthwhile. Many tradeoffs exist. For example, in some cases it may be more effective to make small management adjustments across many stands; in others, it may benefit biodiversity protection more to focus more intensively on specific locations to get the “biggest bang for the buck.” Maintaining high production in portions of the landscape may make it possible to manage the most important locations for biodiversity more strictly to restore and maintain it. Here we outline general procedures that can be employed after such tradeoffs are considered by landowners. More specific guidelines for sustaining particular taxonomic groups are discussed for each group in Sections 6 and 7. These are important to consider as well, especially for the most sensitive species (stream amphibians, non-vascular plants and terrestrial arthropods).

The primary sources of physiological stress in aquatic habitats that can be reduced are excess erosion, sedimentation, or stream temperature increases (Section 6). Maintaining partial canopy cover ameliorates the effects of stream heating caused by canopy removal, and riparian buffer strips up to 30 m wide provide comparable shading to old-growth forest (Beschta et al. 1987). Forest roads may

have a larger effect on both chronic and episodic erosion and sedimentation than harvest alone (Section 6). Minimizing road construction in riparian areas and along steep terrain potentially susceptible to mass failure can significantly reduce potential physiological stress from such effects.

In terrestrial portions of riparian forests, silvicultural treatments of various intensities can create distinct seral environments. Where herbicide use has been applied judiciously, even-aged systems often create floristically diverse early seral communities that have higher herb, shrub, and deciduous tree cover than older stands. These may be biologically rich environments if residual features of the former stand, such as logs, snags, or mature green trees remain. However, the greater variability in temperature in these environments may be detrimental for fungi, bryophytes, and amphibians in all except the mildest climates. Where biological legacies are lacking, they can be comparatively poor habitats for sensitive species. The stem exclusion phase of stand development that occurs after canopy closure following fires or in even-aged silvicultural systems may help shade streams, but may actually be the poorest terrestrial habitat with regard to biodiversity (Gregory et al 1987; Franklin et al. 1997). Dense young stands of conifers often lack horizontal or vertical heterogeneity in structure and composition, resulting in depauperate diversity of shrubs, herbs, and deciduous trees. Management approaches for improving terrestrial conditions include a) maintaining or adding woody debris and creating snags to more closely approximate amounts found where natural disturbance processes have operated at intermediate levels; b) enhancing structural and habitat heterogeneity by planting multiple crop species and/or leaving some native trees unharvested to remain through a second rotation; c) controlling exotic species that act as artificial keystones/pest plants to eliminate artificial keystone threats to biodiversity; d) site-preparation following harvesting that creates conditions that occur with natural disturbances and that conserve coarse woody debris to help maintain many non-crop species; and e) lengthening rotations and developing earlier thinning schedules to increase structural biodiversity. Hartley (2002) describes evidence that these methods do benefit biodiversity and may also entail various economic benefits.

Many of the valuable structural elements and biodiversity associated with early seral communities can be obtained through variable retention systems, which can be designed to cause much less physiological stress on sensitive taxa following harvest. Moreover, retaining legacies from older stands can maintain heterogeneity in structurally simple young conifer plantations (Franklin et al. 1997). Variable retention harvest regimes allow flexibility to plan harvest disturbances to recreate the array of structures and resources created by natural disturbances in indigenous riparian forests. Variable retention strategies spanning the continuum from largely even-aged systems (including shelterwood or seed tree methods) to small patch cuts and light thinning or single tree selection may all be valuable in helping to maintain a spectrum of disturbance sizes and intensities and associated variability in vegetation structure and composition.

Where even-aged management is preferred, extended rotations will enhance protection while integrating riparian management zones into landscapes managed primarily for wood or fiber production. Heterogeneity begets diversity. Therefore, regardless of the primary harvest systems used, biodiversity-oriented riparian management should aim to preserve and create legacies, complex physical and vegetative structures, and as full an array of disturbance regimes as possible.

Riparian buffers reduce erosion and stream temperatures compared to harvesting in close proximity to streams. Effective buffer size will depend on topography and stream size. Effects will be maximized where erosion potential is high, and where removing shade has the biggest effect on stream temperatures (E. Cascades and Klamath regions). In forestlands where variable retention methods are economically viable, a gradient of increasing management intensities from streamside to uplands may be more consistent with intermediate disturbance regime goals due to greater natural disturbance near streams (although streams below impoundments may have low levels of disturbance, and this may not apply). For example, a three-level approach grading from full retention within 30 m of the

streamside to variable retention thinning or patch cuts from 30 to 100 m, and even-aged management beyond 150 m might provide equivalent protection and greater heterogeneity than a fixed 60 m full retention buffer that abuts the intensively managed matrix. Because successful regeneration of tree species like red alder and Douglas fir would be difficult in the first 30 m in this scheme, a landscape view (see Section 11) that allows for periodic regeneration of these zones is also needed.

Initial conditions strongly affect the array of strategies that might be employed to maintain local (alpha) riparian biodiversity. Stands with residual uneven-aged, multi-species forests may be best protected in riparian buffers. At the other extreme, a young, single species conifer plantation may require active thinning or patch cutting to increase growth and crown depth of potentially dominant trees, encourage horizontal and vertical heterogeneity, and favor deciduous trees or shrubs, and herbs. Most managed riparian forests probably fall between these two extremes, and may require a mixture of active or passive management approaches to develop and maintain habitat supporting the full complement of riparian biodiversity.

Given the extremely variable life history traits of the many species inhabiting riparian forests, it is probably inappropriate to assume that we can maintain habitat for all with any single prescription (Huston 1999). For example, a disturbance regime that optimizes understory diversity of vascular plants may be severely detrimental to more sensitive plant or animal species (e.g., liverworts, amphibians), unless sufficient heterogeneity in management is applied, and appropriate scales are considered. Rather, management must encompass sufficient spatial and temporal scale to ensure viability of taxa groups with potentially contrasting needs. This is consistent with maintaining an intermediate disturbance regime as described in Section 3.2. We discuss these topics in the next section on landscape scale approaches for biodiversity protection.

11.0 MULTISCALE MANAGEMENT APPROACHES FOR PROTECTING BIODIVERSITY

To preserve biodiversity, habitat must be maintained for the full complement of species through time and across space. This may be impossible from a stand-scale perspective because a) different species often have conflicting habitat needs; b) different species have different spatial requirements; and c) some species have habitat requirements that require large spatial scales (reviewed by Lindenmayer and Franklin 2002), or are too vulnerable to extinction in landscapes with even low levels of anthropogenic influences (Duffy 2003).

11.1 Modeling Management after Natural Disturbance

Adaptations to recovering from natural disturbances are common. In recent years, a number of books (see Kohm and Franklin 1997; Hunter 1999; Lindenmayer and Franklin 2002), papers (e.g., Atwill 1994), and special features in the journal *Ecological Applications* (Roberts and Gilliam 1995) have addressed the topic of biodiversity in forests managed for fiber production. They have all concluded that management should attempt to deviate less from the historic disturbance regimes in order to better maintain biodiversity. The premise is that organisms are not as well adapted to disturbance regimes that did not occur in the past and/or that substantially diminish various legacies upon which resilience apparently depends. Silviculture based on models of natural stand development following disturbance is now increasingly used where goals are both economic and ecological (Franklin et al. 2002). The general approaches complement and incorporate stand-level procedures such as retaining structures at the time of harvest, use of longer rotations, and active creation of structural complexity and habitat heterogeneity.

In addition, estimates of the historic range of variability in natural disturbances are used to provide general guidance in addressing management questions of how much disturbance and at what spatial

and temporal scales. The scale dependency of historic range of variability can be a limitation, however. For example, at the scale of a small watershed, the proportion of old growth hemlock/Douglas fir may have historically ranged from 0-100%, but its range throughout the whole Douglas fir region probably varied from 30-75% (Lindenmayer and Franklin 2002). In cases where historical information is uncertain or too difficult and/or costly to obtain, managing for an intermediate disturbance regime may be a relatively low risk approach to maintaining biodiversity.

It is beyond the scope of this report to describe the natural range of variation in disturbance regimes that have operated in a region as dynamic as the Pacific Northwest. Appendix B provides a starting point, but managers must gather information on the disturbance regimes in the specific landscape with which they are concerned to use as a basis for aligning treatments. An excellent recent example of this process that can serve as a model for landowners wishing to integrate ecological and economic objectives is provided by Cissell, Swanson, and Weisberg (1999). This approach may be especially well suited for application over relatively large areas with a simple ownership pattern.

It may be easiest to align silviculture with natural disturbance regimes historically characterized by disturbances that created relatively fine-scale age patch mosaics as opposed to large-scale stand replacement or high frequency stand thinning disturbance (Franklin et al. 2002). Harvesting can approximate a patch mosaic in space and time, although patch size tends to be larger with group selection harvesting, and rotation interval for patch establishment tends to be shorter. For emulating large stand replacing disturbances, the challenge is that clearcutting, as traditionally practiced, is described by Franklin et al. (2002) as having little overlap except by creating a light environment suitable for shade-intolerant tree regeneration. Where large stand-replacing disturbances (fire, mass soil movements, large wind throw events) are dominant, they are typically infrequent (i.e., centuries), and they usually leave behind large quantities of wood, and other legacies (i.e., seed released from dormancy) are often present in significant amounts. These differences are also apparent in comparing naturally regenerating post-disturbance stands with plantations. Therefore, in forests where large, stand-replacing disturbances have prevailed, stand-level procedures can be used to help maintain biodiversity, but aligning harvest to natural disturbance may not be cost-effective due to rotation length and retention of wood that accompanies the natural disturbance regime. It may also not be cost-effective to emulate disturbance such as frequent surface fire (e.g., ponderosa pine forests of the eastern Cascades). These fires historically killed non-merchantable sized trees and few large trees.

11.2 Riparian Buffers

Establishing riparian buffers and restricting activities within them is widely regarded as a valuable approach for biodiversity protection, and is the current management paradigm underlying existing riparian management regulations (Section 5). The rationale for these buffers is that streamside vegetation a) prevents water temperatures from becoming too high for fish and amphibians (Beschta et al. 1987); b) provides the nutrient and energy base for streams in the form of allochthonous inputs; and c) is the source of large woody debris that has numerous roles in maintaining biodiversity. Ultimately, the effectiveness of riparian buffers for biodiversity protection depends upon careful consideration of both local site-specific and larger scale conservation goals.

There are both limitations with buffers and potential improvements to consider. As described in Section 5, appropriate widths and activities within buffers are controversial. They are often based on political compromise, rather than on ecological principles. In intensively managed watersheds with simplified stand structures and constraints on natural disturbance processes, buffers may not contain species, structural characteristics, or dynamic processes that provide the intended services. For example, it may be more desirable for woody debris from sources outside of buffers to be placed in streams rather than relying on recruitment from the buffer area. This may be especially true where large conifers are lacking. An additional concern where stream density is high is that management of

the upland forest patches can be impractical or not economically viable. Depending on the condition of these patches, abandoning management may be detrimental to biodiversity. Finally, the functional effects of riparian areas extend to different distances from the stream leading to difficulties in determining appropriate buffer widths. Knutson and Naef (1997, Appendix C, <http://www.wdfw.wa.gov/hab/ripfinal.pdf>) suggest riparian habitat buffer widths for retaining various riparian habitat functions, and these widths vary considerably. Two important sources for this variation are in the research method used and in the ecosystem studied.

Riparian buffers are often uniquely important for terrestrial wildlife, as they often serve as travel corridors (Sections 7.4 and 7.5). Riparian areas at low- to mid-elevations appear to be used more as travel corridors than are riparian areas at high elevations (Kelsey and West 1998); however, the role of stream buffers functioning as travel corridors is not well studied. Using only riparian buffers to provide travel corridors or late-seral forest refugia may not be effective to maintain biodiversity for species that are primarily found in uplands, and perhaps others that use, but do not rely entirely on upslope forests. These tradeoffs need to be considered where upland harvest regimes are designed to compensate for lack of harvest in buffers.

Buffers may be most beneficial for stream amphibians because they are physiologically sensitive, both in streams and in the terrestrial environment near streams. Maximum shading capacity may be reached within a width of 25 m, and 90% of that capacity occurs at 17 m (see Budd et al. 1987; Beschta et al. 1987). However, widths of 30 m or more may be needed if the goal is to stabilize microclimates within some streamside riparian zones (Brososke et al. 1997). Some experts believe that the minimum buffer width may need to be 60-80 m wide (Ledwith 1996a, 1996b; Welsh et al. 1998) or up to 100 m (McComb, McGarigal, and Anthony 1993) to minimize sediment flow, maintain other riparian functions, and protect the most sensitive organisms.

Moreover, as reported in Section 6.2, Welsh and Lind (1996) describe a problem with the misclassification of streams where the faulty assumption is made that aquatic life does not exist in particular channels and this results in inadequate protection for headwater streams. For example, there are concerns that riparian buffer rules for non-fish bearing streams may not be adequate to maintain required microclimatic conditions for the torrent salamander. As mentioned in Section 6.2, forest managers' collective goals may be better served by reducing reliance on a set of physical criteria such as buffer widths at 30 m and by placing more attention on the desired outcomes for streams: a) cool waters (temperature <15 C year round); b) little or no sedimentation; and c) input of large woody debris over the long haul. These issues point to the need to evaluate entire watersheds with regard to present conditions and natural range of variability when considering management that integrates both economic and ecological objectives.

11.3 Reserve-Based Management

Our concept of a reserve is simply a place where the primary goal is biodiversity conservation. Depending on the condition of a reserve, management activities may vary.

It is well known that biodiversity is nonrandomly distributed. Certain sites teem with life, whereas others are relatively species poor. The Nature Conservancy (TNC) and the closely related state Natural Heritage Programs have pioneered an approach to identify sites with exceptional biodiversity on private lands. The approach involves collection of site data and scoring of sites based on their global and state-level biodiversity values. As part of Ecoregional Planning, TNC develops a portfolio of sites that might be managed primarily for conservation via removal from commercial activities. The strength of this approach is that it recognizes the importance of certain sites and includes a mechanism to fund landowners for the financial values of private lands removed from commodity production. Society may be increasingly willing to provide incentives and compensation (<http://www.wa.gov/dnr/htdocs/adm/comm/nr02-92.htm>). Such an approach might have merit if a

trusted nonprofit or government organization could be supported by multiple private forest owners. The conservation value of riparian forests needs to be assessed in this regard on a regional scale. This approach may be best for protecting localized populations of especially rare or sensitive taxa, or exceptionally valuable habitat (i.e., biodiversity “hot spots”, regionally rare habitats such as remnant multi-aged forests). It would be least effective for species with broader home ranges or wider distributions.

Effective biodiversity conservation via reserve networks is a broad planning issue. It needs to be evaluated within a larger landscape program of managed lands that also support some of the values of the reserves, of connectivity and proximity of reserves, of meta-population dynamics, and other issues are beyond the scope of the present analysis.

PART IV PAST, PRESENT, AND FUTURE RESEARCH

12.0 EXISTING LITERATURE AND ONGOING RESEARCH

We searched two databases to assess published and ongoing research as well as taxonomic and geographic patterns of emphasis. For published research, we used the University of Washington/Rocky Mountain Research Station Riparian Bibliography at <http://riaprian.cfr.washington.edu/>, a comprehensive database containing ~12,000 citations, as of March 2003. For ongoing research, we obtained the Forest Research Database, which contains information pertinent to issues in the Pacific Northwest and northern California. This database was created under a contract to the U.S. Environmental Protection Agency in Corvallis, Oregon for the interagency Regional Ecosystem Office (REO) in Portland, Oregon. This database contains descriptions of research projects supporting ecosystem management on both forested and non-forested lands in the region. The information in the database was acquired primarily from responses to a voluntary survey sent to researchers or research institutions in Washington, Oregon, and northern California.

Results of the database searches were not consistent in many respects (Figures 12.1 and 12.2). One reason for this is that the Forest Research Database is not focused solely on riparian research. It was found to contain 120 ongoing projects that involved riparian areas, however, and a number of the projects are oriented toward assessments of ecosystem processes. Many directly deal with components of biodiversity as illustrated in Figure 12.1.

There is clearly an emphasis on endangered species and the related topics of anadromous fish and wildlife in ongoing research (Figure 12.1). The number of studies concerning plants seems surprisingly low, especially considering the growing problem of non-native plants displacing native species and crop species. Considering the ecological importance and diversity of terrestrial invertebrates (Sections 6.3 and 7.5), they clearly lack sufficient attention. Likewise, no studies specifically focusing on non-vascular plants and lichens were found. Although this does not mean that none exist, there is a dearth of attention in terms of actual research devoted to these organisms as further evidenced by published literature. There were no published studies on non-vascular plants, and only two on lichens found in the Riparian Bibliography. The emphasis on endangered species is also not apparent in published literature compared to ongoing research, suggesting this is a relatively recent development. Most published research on elements of biodiversity in riparian areas focuses on plants and wildlife. There is also a considerable amount published on aquatic macroinvertebrates in riparian areas (Figure 12.2).

Beyond what we can say from these data from keyword searches is that another gap in published and ongoing research concerns the difficult issues of landscape-scale processes and planning (see Section 14.0 on future research needs).

Geographic emphasis of ongoing biological research in the Pacific Northwest is shown in Figure 12.3. The Oregon Coast range is receiving more attention than other regions. About twice as many research projects are located in the western Cascades of Washington and Oregon compared to the east side of the range in these states.

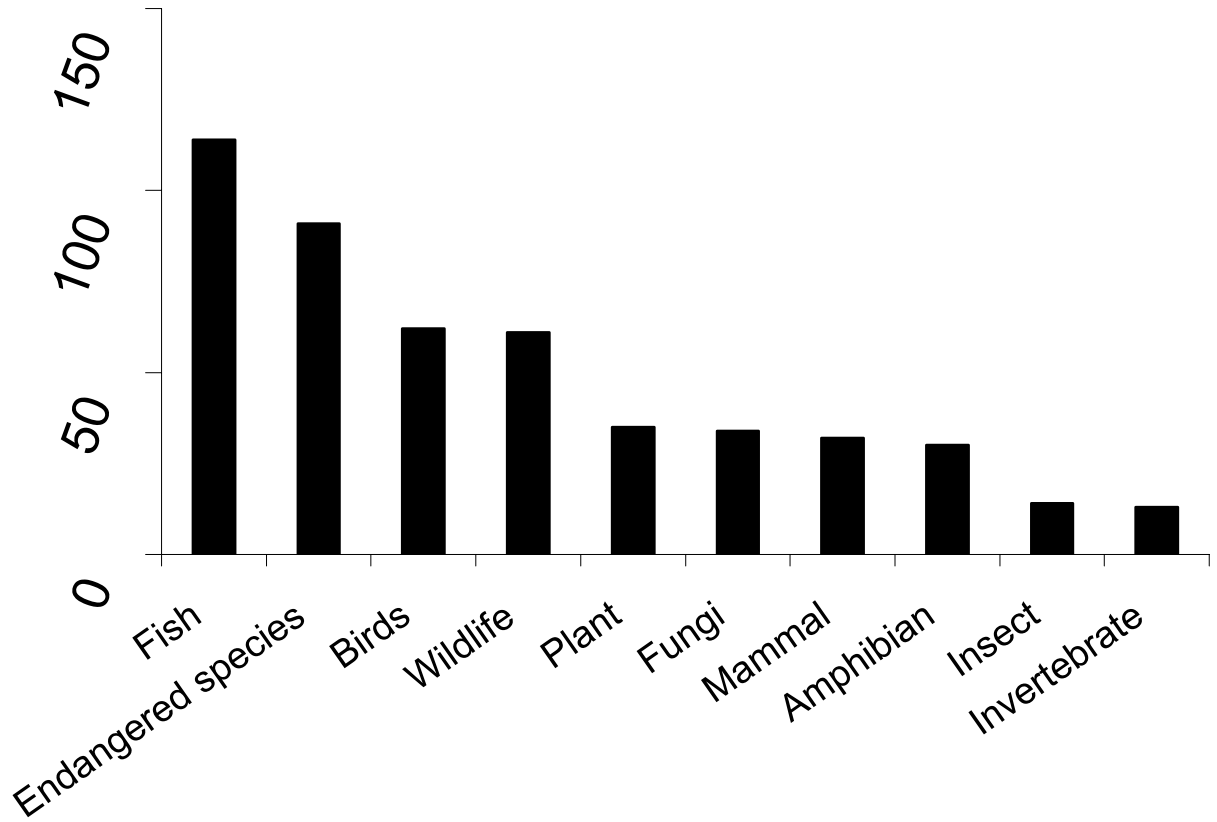


Figure 12.1 Number of Ongoing Studies by Taxonomic Group Identified in the Forest Research Database

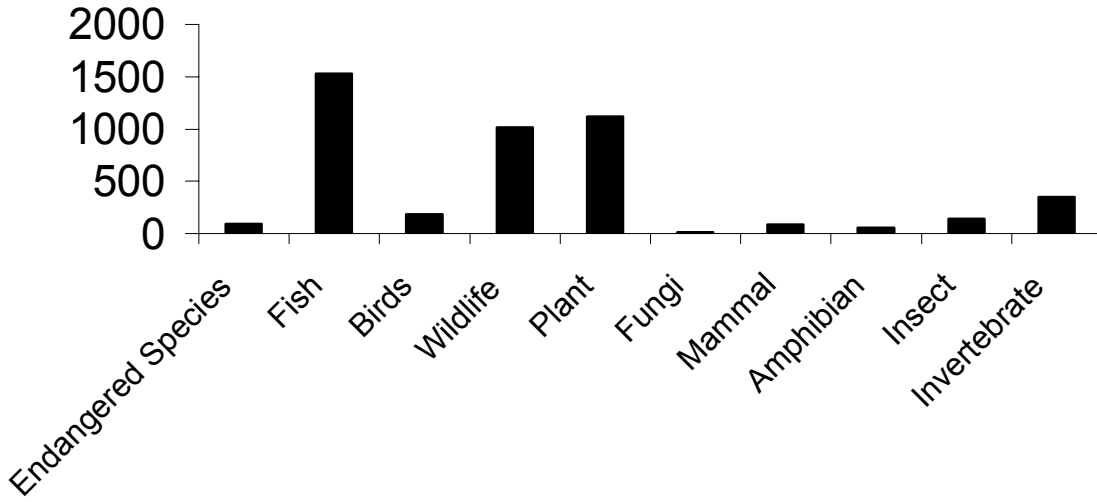


Figure 12.2 Number of Ongoing Studies by Taxonomic Group Identified in the University of Washington/Rocky Mountain Research Station Bibliography

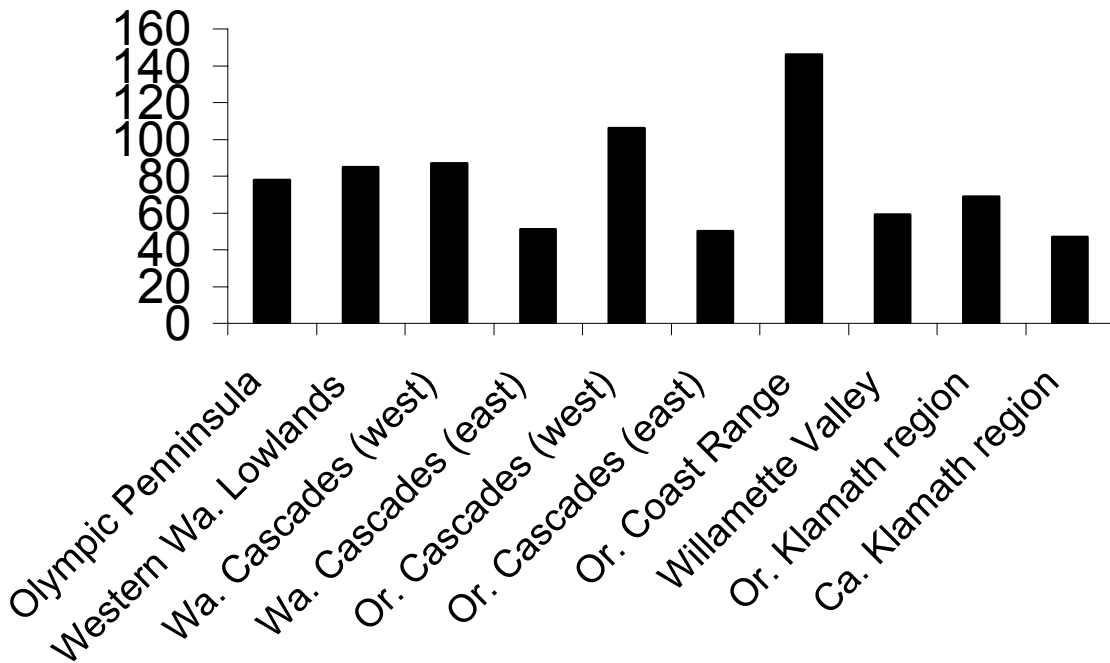


Figure 12.3 Number of Ongoing Studies by Geographic Area Identified in the Forest Research Database

13.0 A MEANS FOR ASSESSING RIPARIAN LITERATURE

Few issues draw sharper reactions from the public and scientific community than timber harvest in the Pacific Northwest. Tensions peak when discussing the management of riparian forests, which contain some of the most productive, biologically rich forests in the region. The perspective that riparian forests require complete protection contrasts with a growing appreciation that riparian forests are structured by disturbance. Although much has been written about riparian forests in the Pacific Northwest, easy answers about forest management effects on biodiversity are elusive. Those interested in determining the effects of forest management on biodiversity must weigh the published literature carefully.

Engeldinger (1991) provided a number of questions for developing annotations and assessing the validity of information sources that are especially useful for considering literature in such contentious fields:

1. Who is the author?
2. What is the author's purpose?
3. Who is the intended audience?
4. What is the author's likely bias, if any?
5. What is the primary information source for the article?
6. What are the primary conclusions?
7. Are the conclusions justified?
8. What is the article's relationship to other sources?

Additional questions might include:

9. Has the article been peer-reviewed?
10. Is the study design robust for addressing the stated objectives?

These and similar questions in critical thinking are dealt with in detail by a number of authors in Shirato (1991). These general principles are highly relevant to an objective assessment of biodiversity protection in riparian management zones. From our review of existing literature and many discussions on the topic, we note several sources of bias or uncertainty in the scientific literature that bear particular consideration.

Political bias. As residents of the region, scientists frequently have strong feelings about land management policies. These feelings run deep with regard to regional rivers and riparian environments. Although most scientists try to maintain neutrality in scientific discussions, advocacy is not unknown (Rykiel 2001). Scientists are increasingly asked to participate in policymaking decisions, especially where important ecological and social values are at stake (Lach et al. 2003). When such decisions impinge upon complex topics such as riparian biodiversity, distinctions between scientists' political perspectives and ecological judgment can become obscured. Some authors assume a protective stance with regard to riparian forests, and argue that any forest management will have a negative effect on biodiversity. Yet, full protection is likely to result in unintended consequences to biological diversity, such as loss of hardwoods over time. Other scientists may emphasize a minimalist perspective on riparian forest protection. Readers should take care to discern when policy perspectives or value judgments become intermixed with scientific discussion.

Taxonomic bias. Disciplinary perspectives strongly infuse the riparian management literature. Fisheries ecology is a particularly strong influence, as are plant ecology, wildlife ecology, and forestry. As noted above, less charismatic or economically valuable taxonomic groups (e.g., soil arthropods) have received much less study, yet these species undoubtedly comprise the majority of species occurring in riparian zones. The tendency to generalize findings from a single group to “biodiversity” as a whole is frequently made in project justification statements and in conclusions of primary papers. As noted above, such cross-taxa inferences are probably not justified in many cases. As we have argued throughout this report, inferences about forest management effects on biodiversity depend on a) the organism's life history; b) the geographic setting; c) previous disturbance regimes; and d) the management intensity. Much more basic research is needed to determine the specific responses of lesser known taxonomic groups and to determine if their responses can be estimated by surrogate species or other metrics.

Geographic bias. As noted above, our knowledge of rare species, riparian dynamics, and forest management research in general, is disproportionately weighted towards sites close to urban centers and research universities (i.e., western Washington, northwest Oregon). Areas east of the Cascades and in the Klamath Region have received less intensive study. More generally, it is probably important to closely consider where the study occurred and to consider whether conclusions can be extrapolated to other locations with sharply contrasting climates, hydrology, or other features.

Generalizations about disturbance effects. The disturbance ecology literature frequently includes clear value judgments that add confusion. In particular, natural disturbance regimes are frequently cited as essential for biodiversity, whereas anthropogenic disturbances are frequently described as ecologically harmful. The fire ecology literature is rife with value judgments such as “cleansing” vs. “catastrophic” wildfire. Until a more quantitative basis for evaluating disturbance mechanisms and taxonomic responses is developed and adhered to, discussions of disturbance ecology will remain imprecise. As we have described, quantifying functional heterogeneity and legacy retention (White and Jentsch 2001) will help explain general effects of disturbance.

14.0 A RESEARCH AGENDA TO SUPPORT RIPARIAN BIODIVERSITY PROTECTION

In this section, we present rationale and recommend approaches for further research in support of biodiversity protection in riparian forests where silviculture is practiced. The recommended research agenda is organized into several programs outlined below, and a number of more taxa-specific research needs. Research needed for specific taxa groups is provided in Sections 6 and 7.

14.1 Programmatic Recommendations

14.1.1 *Program One: Evaluation of Potential and Actual Diversity across Geographic Gradients*

Rationale. There is tremendous spatial variation in the diversity and abundance of native riparian species. We need much more complete information about the factors controlling potential diversity to both locate biodiversity “hot spots” and to assess how current levels of diversity compare with expected values. A research program is needed to more quantitatively define how biodiversity is being affected by forestry practices and to help identify sites of exceptional conservation interest.

Approach. Spatially explicit models could be used to determine distribution and diversity of focal riparian taxa from existing field inventories, augmented with targeted field inventories of poorly understood regions. The survey and manage program on federal lands has begun such an approach. A parallel effort on private lands may also yield valuable insights. Once a response surface of potential diversity had been established for focal groups (e.g., fungi, vascular, nonvascular plants, arthropods), additional field measurements could evaluate sites that are below their biodiversity potential, or that

have regional significance. These insights would add a quantitative basis to statements about the status of biodiversity on private forestlands. Federal inventory and monitoring programs are working to develop this regional understanding of biodiversity to target monitoring efforts (Figure 14.1). Landscape and historical factors strongly govern the potential diversity of a given locale. Once a reliable quantitative estimate of the diversity of a site is obtained, it may be possible to evaluate the deviation between potential an actual diversity of a site.

14.1.2 Program Two: Private Forestlands of the Pacific Northwest

Rationale. Natural disturbance regimes in riparian forests are caused by a complex interplay of fluvial and hillslope disturbance processes. These varied disturbances are known to be important for maintaining the diversity of many types of organisms in riparian forests. Studies of the temporal dynamics of riparian forests have typically taken a single factor approach to the study of disturbance (i.e., fire, fluvial disturbance, gap dynamics). In reality, large landscape-scale disturbances and more localized or low intensity disturbances are both important in terms of their effects on dominance and maintaining habitat heterogeneity in riparian forests (Sakai et al. 1999). When applied uniformly, even-aged or uneven-aged silvicultural systems can both lead to simplified stand structures when contrasted with the patterns caused by stochastic disturbance events. A better understanding of the size, periodicity, and intensity of riparian forest disturbances is needed to inform riparian forest management.

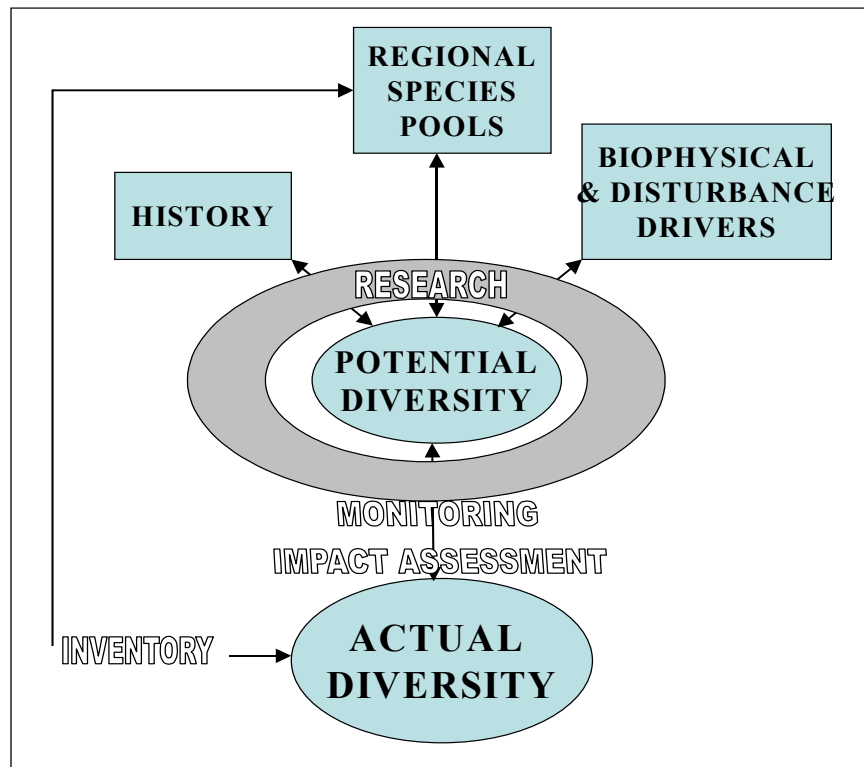


Figure 14.1 Conceptual Model of Controls on Biodiversity, and Roles of Inventory Monitoring, and Research

Approach. Retrospective analyses of radial growth patterns on cut stumps or live trees, hydrologic or climatic analyses, and comparative field studies in remaining reference riparian forest stands and watersheds could be employed to study the complex disturbance regimes and associated stand structures of natural riparian forests. A network of permanent plots added to existing riparian monitoring programs might also provide information on the characteristics of both natural and human-caused disturbances and biological response in these systems.

14.1.3 Program Three: Stand-Scale Analyses of Physiological Stress, Resource Availability, and Species Response across Management Intensity and Macroclimate Gradients

Rationale. Different life forms respond individually to gradients in habitat structure, resource availability, or physiological stress associated with forest management. Quantitative data are needed to determine important stress thresholds for different life form groups across gradients in management intensity. The magnitude of such management-associated changes also varies geographically due to changes in climate and riparian forest structure, such that a management technique (e.g., thinning) that might be relatively innocuous for an element of biodiversity in a mild, coastal climate may be considerably more detrimental in a more severe, interior environment. For example, the response of stream temperature to timber harvest is likely to be considerably greater in the eastern Cascades or Siskiyou than in the Coast Range or Olympic Mountains. A stronger quantitative basis for evaluating physiological stress responses of taxa and associated geographic variation would be a great source of information for private land managers.

Approach. A manipulative study employing a gradient of treatment intensities (e.g., no harvest, light thin, heavy thin, shelterwood, patch cut) replicated in riparian forests across a climate gradient (e.g., Coast Range, Western Cascades, Klamath Mountains, Eastern Cascades) and tracking selected abiotic parameters and elements of riparian biodiversity before and after treatment would provide a rigorous evaluation of such intensity/site interactions.

14.1.4. Program Four: Landscape Integration-Evaluation/Comparison of Conservation Paradigms for Protection of Riparian Biodiversity

Rationale. Although most current regulations target management activities at the stand scale, scientists and land use planners may be able to join forces to develop strategies for planning and integrating stand-scale activities (individual land owner activities) across larger, often multiple ownership landscapes, to evaluate whether the elements critical to landscape-scale biodiversity conservation are also met. There is an increasing realization that conditions of the larger landscape may be as important as local habitat in determining the biodiversity of a site. Multiscale analyses are needed to determine the effective scale of controls on diversity (see Saab 1999). A number of current conservation paradigms in the Pacific Northwest and elsewhere directly influence forest regulations in riparian zones on private lands. As a starting point, we propose three paradigms that warrant comparative study at the landscape scale: natural disturbance regime-based management, riparian buffer systems, and the selection of no harvest preserves. These paradigms are outlined briefly below.

1. Natural disturbance-based management This paradigm proposes to base harvest patterns on an assessment of natural return intervals derived from the landscape disturbance regime. This approach incorporates disturbance as a management tool and attempts to recreate natural spatial patterns of forest age and structure. All areas of the landscape are open to management, but only within the context of natural disturbance intervals and intensities specific to that landscape position.

2. Riparian buffers This paradigm assumes that exclusion or curtailment of management activities within riparian areas is the most prudent means to protect biodiversity in the landscape as a whole. The paradigm has its origins in intensively managed agricultural landscapes, or in landscapes with important coldwater fisheries, where protection of streams is considered paramount.

3. Selection of conservation reserves This paradigm, widely used by the Natural Heritage Program and The Nature Conservancy, assumes that sites with a high concentration of regionally rare or “imperiled” taxa warrant special protection regardless of ownership or landscape position. Protection is advocated through outright land purchase or through conservation easements that preclude future development or extractive management. The reserve system (TNC’s conservation portfolio) so created is intended to conserve regionally and globally significant taxa whether they are riparian-dependent or not.

Approach. These conservation paradigms each involve a number of untested assumptions about the interactions between harvest activities, landscape structure, and species viability. All are well intentioned and actively used in forming riparian management policy or in conservation planning. An explicit comparison of the outcomes of these models in private forest landscapes developed through the use of forest growth and wildlife habitat models would allow us to better assess the strengths and weaknesses of these approaches for maintaining biodiversity in managed landscapes.

14.1.5 Program Five: The Role of Biological Legacies

Rationale. In even-aged, short-rotation forestry, elements of older forests (e.g., large trees, large logs, snags, lichen and fungi populations, seed banks, bud banks) do not have time to develop. The concept of biological legacies, or carryovers from previous stands, has gained increasing attention in recent years (see Lindenmayer and Franklin 2002), yet quantitative data are still needed to guide management and restoration.

Approach. Since retention of certain elements (standing green trees, logs) is costly, it may be valuable to quantify the potential relationships between legacy abundance and specific biodiversity elements. For example, the importance of residual green tree densities for post-harvest lichen diversity may show linear, unimodal, convex, or concave response functions (Figure 14.2). If the linear model applies, more is better. If the convex models applies, much of the positive benefit may occur at lower retention levels. If the concave model applies, high retention levels will be required to maintain lichen diversity. The unimodal model suggests that there is an optimal level of retention for lichen diversity. Understanding these relationships may allow prediction of what different levels of retention do for the maintenance of biodiversity. Direct placement of legacy elements could be a more manipulative approach to evaluating the role of biological legacies (e.g., large wood) for biodiversity (see Hayes and Waldien 2001) that merits further study.

14.1.6 Program Six: Restoration of Riparian Biodiversity

Rationale. Riparian restoration is an active field in the Pacific Northwest, with many projects focusing on salmon and their habitats. A complementary approach might be to explicitly define a number of biodiversity elements (structural heterogeneity, lichen; fungi, small mammal, amphibian, bird abundance and diversity) and attempt to develop trajectories of recovery under alternative active and passive management approaches. Trajectories of recovery are poorly understood for most degraded systems and explicit documentation of recovery is badly needed in impacted landscapes.

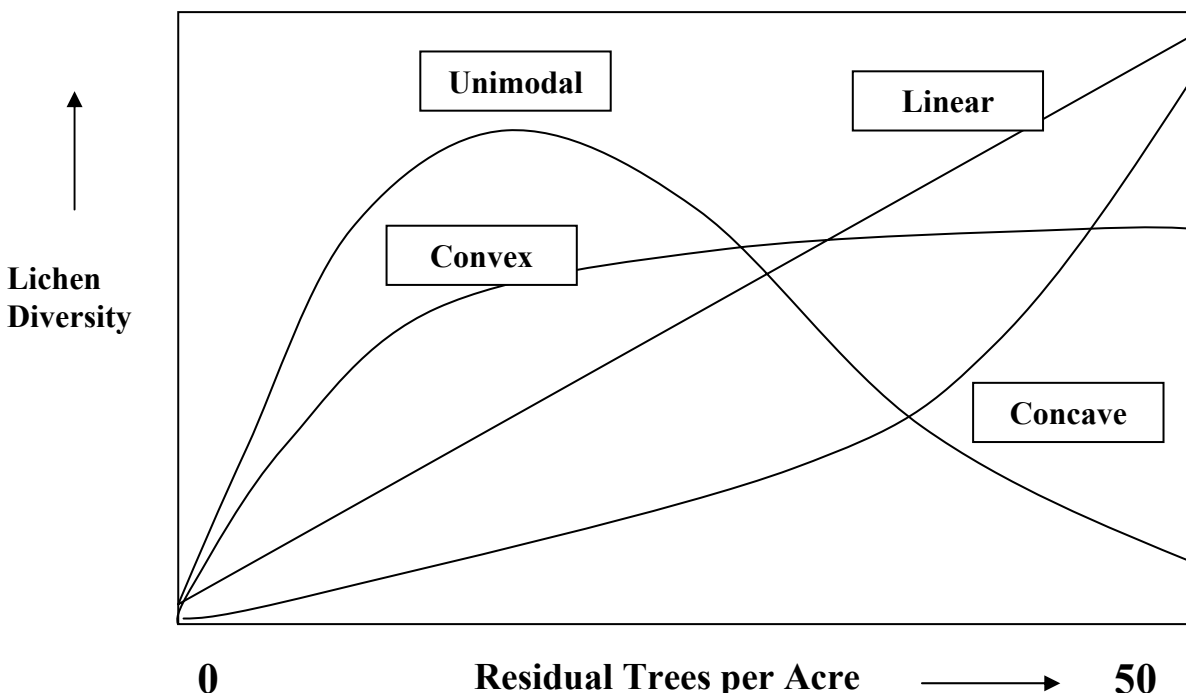


Figure 14.2 Three Potential Response Curves for Lichen Diversity as a Function of Green Tree Retention

The notion of hysteresis, or asymmetry in trajectories of degradation and recovery, is very important in restoration ecology and may provide insights into where to allocate limited restoration funds (Sarr 2002). Systems can have elastic responses to stress, where they recover rapidly and predictably, or plastic response, in which recovery may either be exceedingly slow or impossible (Figure 14.3, Sarr 2002). In a system with an elastic response to stress, the system will probably recover rapidly once the stress is removed. For example, arboreal invertebrate communities would be strongly impacted by a streamside clearcut, but they would probably naturally converge toward the species composition of undisturbed forests with time. Similarly, aquatic invertebrate communities tend to recover rapidly from short pulses of sediment or pollutants. However, in a system with a plastic response, active management may be warranted to ensure or accelerate the recovery of desirable characteristics. This might include aquatic invertebrate or fish communities in a stream that has been eroded to bedrock after splash damming and/or beaver removal. Recovery of the populations will likely first require recovery of habitat structure and function, or at least an approximation of it.

Better understanding of essential species or ecosystem elements (“keystones”) and recovery responses of target taxa would provide a better ability to forecast where active or passive restoration approaches are needed. Finally, documentation of species’ responses to complete cycles of degradation and recovery (e.g., fire, debris flow cycles) may be essential to fully understand the life history requirements of certain species.

Approach. Once restoration goals are clearly defined, modeling or long-term manipulative field studies could be used to determine recovery trajectories for large wood (Beechie et al. 2000) or other target elements of biodiversity. The manipulative studies could use either silvicultural or other methods to augment recovery. For example, Hibbs and Chan (1997) noted that overstory thinning and understory shrub cutting both increased survival and growth of understory conifers. Placement of large wood on the riparian forest floor or creating artificial cavities in trees could also be evaluated as

a means of rebuilding depressed wildlife or populations in riparian forests. Manipulative restoration experiments that add critical elements (beavers, large wood, mycorrhizal species) or remove non-native species (cowbirds, Himalayan blackberry, giant reed) could provide the means to unambiguously identify keystone species or processes that have an exception effect on the recovery of riparian biodiversity.

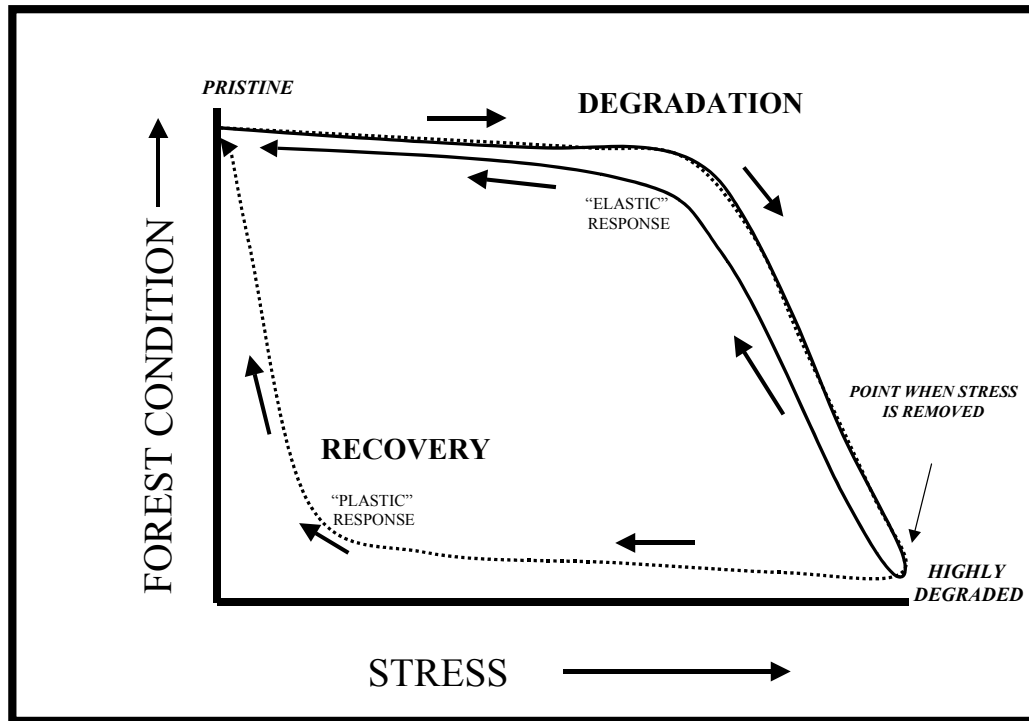


Figure 14.3 Conceptual Models of Physiological Stress and Recovery in a Riparian System (based on Sarr 2002)

In addition, the permanent plot monitoring system mentioned above would provide important insights into natural patterns of degradation and recovery that maintain biodiversity and could guide ecological restoration.

14.1.7 Additional Taxa Specific Recommendations

Additional taxa-specific recommendations can be found at the conclusions of each taxon subsection in Sections 6 and 7. A common information need for nearly all taxa groups is a better understanding of the individual species groups away from intensively studied locales, and more effort to determine the interactions between forest management and species diversity in a variety of settings. Program 3 above may provide a means to address some of these concerns. In addition to the need for more basic life history information, the subsection authors also highlighted the need to better determine the severity and duration of management effects, and the need to frame questions at the landscape scale to determine the factors maintaining the viability of species populations. Program 4 above may partially address these needs.

REFERENCES

- Adams, M.J., and R.B. Bury. 2002. The endemic headwater stream amphibians of the American Northwest: association with environmental gradients in a large forest reserve. *Global Ecology and Biogeography* 11: 169-178.
- Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Washington, D.C.: Island Press.
- Albini, F., M. Ruhul Amin, R.D. Hungerford, W.H. Frandsen, and K.C. Ryan. 1996. *Models for fire-driven heat and moisture transport in soils*. USDA Forest Service, General Technical Report INT-GTR-335.
- Amaranthus, M.P., and D.A. Perry. 1987. Effect of soil transpiration on ectomycorrhizae formation on the survival and growth of conifer seedlings in old non-reforested clearcuts. *Canadian Journal of Forest Research* 17: 944-950.
- Anderson, N.H. 1992. Influence of disturbance on insect communities in Pacific Northwest streams. *Hydrobiologia* 248: 79-92.
- Anderson, N.H., and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology* 24: 351-377.
- Anthony, R.G., and F.B. Isaacs. 1989. Characteristics of bald eagle nest sites in Oregon. *Journal of Wildlife Management* 53: 148-159.
- Anthony, R.G., M.A. O'Connell, M.M. Pollock, and J.G. Hallett. 2003. Associations of mammals with riparian ecosystems in Pacific Northwest forests. In *Mammalian community dynamics: Management and conservation in the coniferous forests of western North America*, ed. C.J. Zabel and R.G. Anthony, 510-563. Cambridge, UK: Cambridge University Press.
- Antvogel, H., and A. Bonn. 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography* 24: 470-482.
- Arnett, E.B., R.J. Anderson, C. Sokol, F.B. Isaacs, R.G. Anthony, and W.P. Erickson. 2001. Relationships between nesting bald eagles and selective logging in south-central Oregon. *Wildlife Society Bulletin* 29: 795-803.
- Atwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management* 63: 247-300.
- Bailey, J.D., C. Mayrsohn, P. Doescher, E. St. Pierre, and J.C. Tappeiner II. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. *Forest Ecology and Management* 112: 289-302.
- Baker, W.L. 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Association of American Geographers* 79: 65-78.
- Baker, W.L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research* 31: 1205-1226.
- Barbour, M.G., and J. Major. 1977. *Terrestrial vegetation of California*. New York: John Wiley and Sons.

- Beach, E.W., and C.B. Halpern. 2001. Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate, and vegetation. *Canadian Journal of Forest Research* 31: 471-483.
- Beacham, T.D., and C.B. Murray. 1987. Adaptive variation in body size, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 244-261.
- Beechie, T.J., G. Pess, P. Kennard, R.E. Bilby, and S. Bolton. 2000. Modeling recovery rates and pathways for woody debris recruitment in northwestern Washington streams. *North American Journal of Fisheries Management* 20: 436-452.
- Benckiser, G. 1997. *Fauna in soil ecosystems: Recycling processes, nutrient fluxes and agricultural production*. Monticello, NY: Dekker Press.
- Benda, L., T.J. Beechie, R.C. Wissmar, and A. Johnson. 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river basin, Washington state, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 79: 1246-1256.
- Benda, L.E., P. Bigelow, and T.M. Worsley. 2002. Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, U.S.A. *Canadian Journal of Forest Research* 32: 1460-1477.
- Bendix, J. 1994. Scale, direction, and pattern in riparian vegetation-environment relationships. *Annals of the Association of American Geographers* 84: 652-665.
- . 1997. Flood disturbance and the distribution of riparian species diversity. *The Geographical Review* 87: 468-483.
- . 1998. Impact of a flood on southern California riparian vegetation. *Physical Geography* 19: 162-174.
- Beschta, R.L., and W.S. Platts. 1986. Morphological features of small streams: Significance and function. *Water Resources Bulletin* 22: 369-379.
- Beschta, R.L., R.E. Bilby, G.W. Brown, L.B. Holtby, and T.D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. In *Streamside management: Forestry and fishery interactions*, ed. E.O. Salo and T.W. Cundy, 191-232. Institute of Forest Resources Contribution 57. University of Washington, College of Forest Resources, Seattle, WA.
- Beschta, R.L., J.J. Rhodes, R. Gresswell, J.B. Kauffman, G.W. Minshall, R. Hauer, J.Karr, D. Perry, and C. Frissell. 2004. Postfire management on forested public lands of the western USA. *Conservation Biology* 18: 957-967.
- Bestelmeyer B.T., J.R. Miller, and J.A. Wiens 2003. Applying species diversity theory to land management. *Ecological Applications* 13: 1750-1761.
- Biek, R., L.S. Mills, and R.B. Bury. 2002. Terrestrial and stream amphibians across clearcut-forest interfaces in the Siskiyou Mountains, Oregon. *Northwest Science* 76: 129-140.
- Bilby, R.E. K. Sullivan, and S.H. Duncan. 1989. The generation and fate of road-surface sediment in forested watershed in southwestern Washington. *Forest Science* 35(2): 453-468.
- Bilby, R.E., and J.W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2499-2508.

- Bilby, R.E., and P.A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 540-551.
- . 1998. Hydrology. In *River ecology and management: Lessons from the Pacific coastal ecoregion*, ed. R.J. Naiman, and R.E. Bilby, 373-398. New York: Springer-Verlag.
- Bird, S., R.N. Coulson, and D.A. Crossley, Jr. 2000. Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. *Forest Ecology and Management* 131: 65-80.
- Bisson, P.A., and J.R. Sedell. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. In *Fish and wildlife relationships in old-growth forests*, ed. W.R. Meehan, T.R. Merrell and T.A. Henley, 121-129. Morehead City, NC: American Institute of Fishery Research Biologists.
- Bisson, P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grete, R.A. House, M.L. Murphy, K.V. Koski, and J.R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. In *Streamside management: Forestry and fishery interactions*, ed. E.O. Salo and T. W. Cundy, 143-190. Institute of Forest Resources Contribution 57. University of Washington, College of Forest Resources, Seattle, WA.
- Bisson, P.A., T.P. Quinn, G.H. Reeves, and S.V. Gregory. 1992. Best management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest river systems. In *Watershed management: Balancing sustainability and environmental change*, ed. R.J. Naiman, 189-232. New York: Springer-Verlag.
- Blaustein, A.R., J.J. Beatty, D.H. Olson, and R.M. Storm. 1995. *The biology of amphibians and reptiles in old growth forests in the Pacific Northwest*. USDA Forest Service General Technical Report PNW-GTR-337, Pacific Northwest Research Station, Portland, OR.
- Bond, W.J. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society, London B* 334: 83-90.
- Brandner, T.A., R.O. Peterson, and K.L. Risenhoover. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology* 71: 155-164.
- Brenner, G. J. 2000. Riparian and adjacent upslope beetle communities along a third order stream in the western Cascade Mountain Range, Oregon. Ph.D. diss., Oregon State University, Corvallis, OR.
- Brinson, M.M., and J. Verhoeven. 1999. Riparian forests. In *Maintaining biodiversity in forest ecosystems*, ed. M.L. Hunter, 265-299. Cambridge, UK: Cambridge University Press.
- Brodo, I.M., S.D. Sharnoff, and S. Sharnoff. 2001. *Lichens of North America*. New Haven, CT: Yale University Press.
- Brookshire, E., N. Jack, J.B Kauffman, D. Lytjen, and N. Otting. 2002. Cumulative effects of wild ungulate and livestock herbivory on riparian willows. *Oecologia* 132: 559-566.
- Brosofske, K.B., J. Chen, R.J. Naiman, and J.F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* 7: 1188-1200.
- Brown, G.W., and J.T. Krygier. 1970. Effects of clear-cutting on stream temperature. *Water Resources Research* 6: 1133-1139.

- Brown, H.A. 1975. Temperature and the development of the tailed frog, *Ascaphus truei*. *Comparative Biochemistry and Physiology* 50A: 397-405.
- Brown, H.A. 1989. Developmental anatomy of the tailed frog (*Ascaphus truei*): a primitive frog with large eggs and slow development. *Journal of the Zoological Society of London* 217: 525-537.
- Brown, H. A. 1990. Morphological variation and age-class determination in overwintering tadpoles of the tailed frog *Ascaphus truei*. *Journal of the Zoological Society of London* 220: 171-184.
- Brown, J.K., E.D. Reinhardt, and K.A. Kramer. 2003. *Coarse woody debris: Managing benefits and fire hazard in the recovering forest*. USDA Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-105.
- Budd, W.M., P.L. Cohen, P.R. Saunders, and F.R. Steiner. 1987. Stream corridor management in the Pacific Northwest: I. Determination of stream-corridor widths. *Environmental Management* 11: 587-597.
- Buehler, D.A. 2000. Bald Eagle (*Haliaeetus leucocephalus*). No. 506 in *The birds of North America*, ed. A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington D.C.
- Bull, E.L., and B.E. Carter. 1996. *Tailed frogs: distribution, ecology, and association with timber harvest in northeastern Oregon*. USDA Forest Service, Pacific Northwest Research Station Report PNW-RP-497.
- Bunnell, F.L., L.L. Kremsater, and E. Wind. 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands. *Environmental Review* 7: 97-146.
- Bury, R.B. 1972. Small mammals and other prey in the diet of the Pacific giant salamander (*Dicamptodon ensatus*). *American Midland Naturalist* 87: 524-526.
- . 1994. Vertebrates in the Pacific Northwest: Species richness, endemism and dependency on old-growth forests. In *Biological diversity: Problems and challenges*, ed. S.K. Majumdar, D.J. Brenner, J.E. Lovich, and J.F. Schalles, 392-404. Easton, PA.: Pennsylvania Academy of Sciences.
- Bury, R.B., and P.S. Corn. 1987. Evaluation of pitfall arrays to sample small vertebrates in Pacific Northwest forests. *Journal of Wildlife Management* 51: 112-117.
- . 1988a. Responses of aquatic and streamside amphibians to timber harvest: A review. In *Streamside management: Riparian wildlife and forestry interaction*, ed. K. Raedeke, 165-184. University of Washington, Institute of Forest Resources, Contribution No. 59.
- . 1988b. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. In *Management of amphibians, reptiles, and small mammals in North America*, ed. R.C. Szaro, K.E. Severson and D.R. Patton, 11-22. USDA Forest Service General Technical Report RM-GTR-166.
- Bury, R.B., P.S. Corn, F.F. Gilbert, and L.L.C. Jones. 1991. Aquatic amphibian communities in Oregon and Washington. In *Wildlife and vegetation of unmanaged Douglas-fir forests*, L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff, Technical Coordinators, 352-362. USDA Forest Service General Technical Report PNW-GTR-285.
- Bury, R.B., and C.A. Pearl. 1999. Klamath-Siskiyou herpetofauna: biogeographic patterns and conservation strategies. *Natural Areas Journal* 19: 341-350.

- Bury, R.B., and M.J. Adams. 1999. Variation in age at metamorphosis across a latitudinal gradient for the tailed frog, *Ascaphus truei*. *Herpetologica* 55: 283-291.
- Byrd, K.B., V.T. Parker, D.R. Vogler, and K.W. Cullings. 2000. The influence off clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming, and Gallatin National Forest, Montana. *Canadian Journal of Botany* 78: 149-156.
- Campbell, A.G., and Franklin, J.F. 1979. *Riparian vegetation in Oregon's western Cascade Mountains: composition, biomass, and autumn phenology*. U.S. I.P.B. Program Bulletin No. 14, Coniferous Forest Biome, Ecosystem Analysis Studies.
- Carey, A.B., and R.O. Curtis. 1996. Conservation of biodiversity: a useful paradigm for forest ecosystem management. *Wildlife Society Bulletin* 24: 610-620.
- Carl, L.M., and M.C. Healey. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of chinook salmon (*Oncorhynchus tshawytscha*) in the Nanaimo River, British Columbia. *Canadian Journal of Fisheries and Aquatic Science* 41: 1070-1077.
- Carlton, G.C. 1989. The structure and dynamics of red alder communities in the central Coast Range of Oregon. M.S. thesis, Oregon State University, Corvallis, OR.
- Caselle, J.E., and R.R. Warner. 1996. Variability in recruitment of coral reef fishes: The importance of habitat at two spatial scales. *Ecology* 77: 2488-2504.
- Castelle, A.J. and A.W. Johnson. 2000. *Riparian vegetation effectiveness*. NCASI Technical Bulletin 799, Research Triangle Park, NC: National Council of the Paper Industry for Air and Stream Improvement, Inc.
- Chamberlin, T.W., R.D. Harr, and F.H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. In *Influences of forest and rangeland management on salmonid fishes and their habitats*, Special Publication 19, ed. W. R. Meehan, 181-206. Bethesda, MD: American Fisheries Society.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.
- Christensen, N.L. 1991. Wilderness and high intensity fire: How much is enough. In *Proceedings of the 17th Tall Timbers Fire Ecology Conference*, 9-24. May, 1989. Tall Timbers Research Station, Tallahassee, Florida.
- Christy, R.E., and S.D. West. 1993. *Biology of bats in Douglas-fir forests*. USDA Forest Service General Technical Report, PNW-GTR-308.
- Cissell, J. H., F.J. Swanson, F. J., and P.J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, Oregon. *Ecological Applications* 9: 1217-1231.
- Clark, J.S., J. Mohan, M. Dietze, and I. Ibanez. 2003. Coexistence: How to identify trophic trade-offs. *Ecology* 84: 17-31.
- Claussen, D.L. 1973. The thermal relations of the tailed frog, *Ascaphus truei*, and the Pacific treefrog, *Hyla regilla*. *Comparative Biochemistry and Physiology* 44A: 137-153.
- Cohen, W.B., T.A. Spies, R.J. Alig, D.R. Oetter, T K. Maiersperger, and M. Fiorella. 2002. Characterizing 23 years (1972-95) of stand replacement disturbance in western Oregon forests with Landsat imagery. *Ecosystems* 5: 122-137.

- Coleman, D.C., and D.A. Crossley, Jr. 1996. *Fundamentals of soil ecology*. New York: Academic Press.
- Collinge, S.K., M. Holyoak, C.B. Barr, and J.T. Marty. 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. *Biological Conservation* 100: 103-113.
- Collins, S.L., P.G. Risser, and E.L. Rice. 1981. Ordination and classification of mature bottomland forests in northcentral Oklahoma. *Bulletin of the Torrey Botanical Club* 108: 152-165.
- Connell, J.H. 1978. Diversity in tropical forests and coral reefs. *Science* 199: 1302-1309.
- Corn, P.S., and R.B. Bury. 1989. Logging in western Oregon: Responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29: 1-19.
- . 1991. Terrestrial amphibian communities in the Oregon Coast Range. In *Wildlife and vegetation of unmanaged Douglas-fir forests*, L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff, Technical Coordinators, 305-317. USDA Forest Service, General Technical Report, PNW-GTR-285.
- Corn, P.S., R.B. Bury, and E.J. Hyde. 2003. Conservation of North American stream amphibians. In *Amphibian conservation*, ed. R. Semlitsch, 24-36. Washington DC: Smithsonian Institution Press.
- Currie, D.J. 1991. Energy and large-scale patterns of animal and plant species richness. *American Naturalist* 137: 27-49.
- Daugherty, D.H., and A. Sheldon. 1982. Age determination, growth, and life history of a Montana population of the tailed frog (*Ascaphus truei*). *Herpetologica* 38: 461-468.
- Davis, G.W., D.M. Richardson, J.E. Keeley, and R.J. Hobbs. 1996. Mediterranean-type ecosystems: The influence of biodiversity on their functioning. In *Functional roles of biodiversity: A global perspective*, ed. H. A. Mooney, J. H. Cushman, E. Medina, O.E. Sala and E.D. Schulze, 152-183. New York: John Wiley and Sons Ltd.
- de Vlaming, V., and R.B. Bury. 1970. Thermal selection in tadpoles of the tailed frog, *Ascaphus truei*. *Journal of Herpetology* 4: 179-189.
- Deal, R.L. 1997. *Understory plant diversity in riparian alder-conifer stands after logging in southeast Alaska*. USDA Forest Service, Pacific Northwest Research Station, Research Note PNW-RN-523.
- Decocq, G. 2002. Patterns of plant species and community diversity at different organizational levels in a forested riparian landscape. *Journal of Vegetation Science* 13: 91-106.
- Deharveng, L. 1996. Soil Collembola diversity, endemism, and reforestation: a case study in the Pyrenees (France). *Conservation Biology* 10: 74-84.
- deMaynadier, P.G., and M.L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the literature. *Environmental Reviews* 3: 230-261.
- den Boer, P.J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18: 165-194.
- Desender, K. 1994. *Carabid beetles: Ecology and evolution*. Dordrecht, Netherlands: Kluwer Academic Press.

- Diller, L.V., and R.L. Wallace. 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. *Journal of Herpetology* 30: 184-191.
- Dix, N. J., and J. Webster. 1995. *Fungal ecology*. New York: Chapman and Hall.
- Doyle, A.T. 1990. Use of riparian and upland habitats by small mammals. *Journal of Mammalogy* 71: 14-23.
- Duffy, J.E. 2003. Biodiversity loss, trophic skew and ecosystem function. *Ecology Letters* 6: 680.
- Dupuis, L., and D. Steventon. 1999. Riparian management and the tailed frog in northern coastal forests. *Forest Ecology and Management* 124: 35-43.
- Durall, D.M., M.D. Jones, E.F. Wright, P. Kroeger, and K.D. Coates. 1999. Species richness of ectomycorrhizal fungi in cutblocks of different sizes in the interior cedar-hemlock forests of northwestern British Columbia: sporocarps and ectomycorrhizae. *Canadian Journal of Forest Research* 29: 1322-1332.
- Dwire, K.A., and J.B. Kauffman. 2003. Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management* 178: 61-74.
- Edwards, R.T. 1998. The hyporheic zone. In *River ecology and management: Lessons from the Pacific coastal ecoregion*, ed. R.J. Naiman and R.E. Bilby, 399-429. New York: Springer-Verlag.
- Elton, C.S. 1958. *The Ecology of invasions by animals and plants*. London: Methuen Publishing.
- Engeldinger, E. 1991. Bibliographic instruction and the teaching of critical thinking. In *Judging the validity of information sources: Teaching critical analysis in bibliographic instruction*, ed. L. Shirato, 29-46. Ann Arbor, MI: Pierian Press.
- Englund, G. 1991. Effects of disturbance on stream moss and invertebrate community structure. *Journal of the North American Benthological Society* 10: 143-153.
- Erickson, J.L., and S.D. West. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation* 109: 95-102.
- Erman, D.C., J.D. Newbold, and K.B. Roby. 1977. *Evaluation of streamside bufferstrips for protecting aquatic organisms*. Contribution 165. California Water Resource Center, University of California, Davis.
- Erwin, T.L., G.E. Ball, and D.R. Whitehead. 1979. Carabid beetles: their evolution, natural history and classification. In *Proceedings of the first international symposium. Carabidology*, Smithsonian Institution. Washington, D. C. Aug 21-25, 1976. The Hague, Netherlands: Dr. Junk Publications.
- Estes, J.A., and J.F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185: 1058-1060.
- Estrada-Venegas, E.G. 1995. Soil arthropods in the central Cascades: Slash burning effects and biology of some species. M.S. thesis, Oregon State University, Corvallis, OR.
- Everest, F.H., R.L. Beschta, J.C. Scrivener, K.V. Koski, J.R. Sedell, and C.J. Cederholm. 1987. Fine sediment and salmonid production: A paradox. In *Streamside management: Forestry and fishery interactions*, ed. E.O. Salo and T.W. Cundy, 98-142. Institute of Forest Research Contribution 57. University of Washington, College of Forest Resources, Seattle, WA.

- Everett, R.L., R. Schellhaas, P. Ohlson, D. Spurbeck, and D. Keenum. 2001. *Continuity in fire disturbance between riparian and adjacent sideslopes in the Douglas-fir forest series*. <http://www.fs.fed.us/pnw/pubs/journals/riparian.pdf> (accessed September 28, 2005).
- Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. *Geomorphology* 13: 133-144.
- Findlay, S.E.G., and T.L. Arsuffi. 1989. Microbial growth and detritus transformations during decomposition of leaf litter in a stream. *Freshwater Biology* 21: 112-115.
- Fonda, R.W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* 55: 927-942.
- Forman, R.T.T., D. Sperling, J.H. Bissonette, A.P. Clevenger, C.D. Cutshall, V.H. Dale, L. Fahrig, R. France, C.R. Goldman, K. Heanue, J.A. Jones, F.J. Swanson, T. Turrentine, and T.C. Winter. 2003. *Road ecology: Science and solutions*. Covelo, CA: Island Press.
- Forsey, E.S., and E.M. Baggs. 2001. Winter activity of mammals in riparian zones and adjacent forests prior to and following clear-cutting at Copper Lake, Newfoundland, Canada. *Forest Ecology and Management* 145: 163-171.
- Frandsen, W.H., and K.C. Ryan. 1986. Soil moisture reduces belowground heat flux and soil temperatures under a burning fuel pile. *Canadian Journal of Forest Research* 16: 244-248.
- Franklin, J.F. 1992. Scientific basis for new perspectives. In *Watershed management: Balancing sustainability and environmental change*, ed. R. Naiman, 5-72. New York: Springer-Verlag.
- Franklin, J.F., and C.T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Corvallis OR: Oregon State University Press.
- Franklin, J.F., D.R. Berg, D.A. Thornburgh, and J.C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. In *Creating a forestry for the 21st Century*, ed. K.A. Kohm and J.F. Franklin, 111-140. Covelo, CA: Island Press.
- Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berge, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155: 399-423.
- Frest, T.J. 2002. Native snails: Indicators of ecosystem health. *Wild Earth* 12: 44-50.
- Frissell, C.A. 1993. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (U.S.A.). *Conservation Biology* 7: 342-354.
- Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management* 10:199-214.
- Gaines, S.D., and M.W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: Extremes in ecology. *Ecology* 74:1677-92.
- Garrett, M.G., J. W. Watson, and R.G. Anthony. 1993. Bald eagle home range and habitat use in the Columbia River estuary. *Journal of Wildlife Management* 57: 19-27.

- Gecy, J.L., and M.V. Wilson. 1990. Initial establishment of riparian vegetation after disturbance by debris flows in Oregon. *American Midland Naturalist* 123: 282-291.
- Geppert, R.R., C.W. Lorenz, and A.G. Larson. 1985. *Cumulative effects of forest practices on the environment: A state of the knowledge*. Washington Forest Practices Board Project No. 0130, Department of Natural Resources, Olympia, WA.
- Gharrett, A.J., and W.W. Smoker. 1993. Genetic components in life-history traits contribute to population structure. In *Genetic conservation of salmonid fishes*, ed. J.J. Cloud and G.H. Thorguard, 197-202. New York: Plenum Press.
- Gibbons, D.R., and E.O. Salo. 1973. *An annotated bibliography of the effects of logging on fish of the western United States and Canada*. USDA Forest Service General Technical Report. PNW-10.
- Glime, J.M., and Vitt, D.H. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. *Canadian Journal of Botany* 65: 1824-1837.
- Gomez, D.M., and R.G. Anthony. 1998. Small mammal abundance in riparian and upslope areas of five seral stages in western Oregon. *Northwest Science* 72: 293-302.
- Good, D.A., and D.B. Wake. 1992. Geographic variation and speciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). *University of California Publications in Zoology* 126: 1-91.
- Goodman, D.M., and J.A. Trofymow. 1998. Comparison of communities of ectomycorrhizal fungi in old-growth and mature stands of Douglas-fir at two sites on southern Vancouver Island. *Canadian Journal of Forest Research* 28: 574-581
- Graecen, E.L., and R. Sands. 1980. Compaction of forest soils: A review. *Australian Journal of Soil Research* 18:163-189.
- Grafius, E. 1976. The conversion of allochthonous material by stream detritivores. M.S. thesis, Oregon State University, Corvallis, OR.
- Grant, G.E., and F.J. Swanson. 1995. Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. In *Natural and anthropogenic influences in fluvial geomorphology: The Wolman volume*. Geophysical Monograph 89, ed. J.E. Costa, A.J. Miller, K.W. Potter, and P. Wilcock, 83-101. Washington, DC: American Geophysical Union.
- Gray, J.R.A., and J.M. Edington. 1969. Effect of woodland clearance on stream temperature. *Journal of the Fisheries Research Board of Canada* 26: 399-403.
- Gregory, S.V. 1997. Riparian management in the 21st century. In *Creating a forestry for the 21st century*, ed. K. A. Kohm and J. F. Franklin, 69-86. Covelo CA: Island Press.
- Gregory, S.V., G.A. Lamberti, D.C. Erman, K.V. Koski, M.L. Murphy, and J.R. Sedell. 1987. Influence of forest practices on aquatic production. In *Streamside management: Forestry and fishery interactions*, ed. E.O. Salo and T.W. Cundy, 233-255. Institute of Forest Resources Contribution 57. University of Washington, College of Forest Resources, Seattle, WA.
- Gregory, S.V., and L. Ashkenas. 1990. *Riparian management guide: Willamette National Forest*. USDA Forest Service, Pacific Northwest Region, Corvallis, OR.
- Gregory, S.V., F. J. Swanson, W. A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* 41 8: 540-551.

- Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* 128: 193-221.
- Grier, C.C., and S.W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* 58: 893-899.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Grindal, S.D. 1998. Habitat use by bats in second- and old-growth stands in the Nimpkish Valley, Vancouver Island. *Northwest Science* 72 (Special Issue No. 2): 116-118.
- Hagans, D.K., W.E. Weaver, and M.A. Madej. 1986. Long-term on-site and off-site effects of logging and erosion in the Redwood Creek Basin, northern California. In *Papers presented at the American Geophysical Union meeting on cumulative effects*, NCASI Technical Bulletin No. 490, pp. 38-65. New York: National Council of the Paper Industry for Air and Stream Improvement, Inc.
- Hagar, J.C. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. *Journal of Wildlife Management* 63: 484-496.
- Hagar, J.C., W.C. McComb, and W.H. Emmingham. 1996. Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. *Wildlife Society Bulletin* 24: 353-366.
- Hagerman, S.M., S.M. Sakakibara, and D.M. Durall. 2000. Potential for woody understorey plants to provide refuge for ectomycorrhizal inoculum at an Interior Douglas-fir forest after clearcut logging. In *Proceedings, From science to management and back: Aa science forum for southern interior ecosystems of British Columbia*, ed. C. Hollstedt, K. Sutherland, and T. Innes, 131-135. Kamloops, B.C.: Southern Interior Forest Extension and Research Partnership.
- Hairston-Strang, A.B., and P.W. Adams. 1998. Potential large woody debris sources in riparian buffers after harvesting in Oregon, U.S.A. *Forest Ecology and Management* 112: 67-77.
- Hall, J.D., and R.L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams. In *Symposium on salmon and trout in streams*, ed. T. G. Northcote, 335-375. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C.
- Hall, J.D., M.L. Murphy, and R.S. Aho. 1978. An improved design for assessing impacts of watershed practices on small streams. *Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen* 20: 1359-1365.
- Hall, J.D., P.A. Bisson, and R.E. Gresswell, eds. 1997. *Sea-run cutthroat trout: Biology, management, and future conservation*. Corvallis, OR: Oregon Chapter, American Fisheries Society.
- Hankin, D.G., J.W. Nicholas, and T.W. Downey. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 50: 347-358.
- Hansen, A.J., T.A. Spies, F.J. Swanson, and J.L. Ohmann. 1991. Conserving biodiversity in managed forests: Lessons learned from natural forests. *BioScience* 41: 382-392.
- Hansen, A.J., and J. Rotella. 1999. Abiotic factors. In *Maintaining biodiversity in forest ecosystems*, ed. M. Hunter, 161-209. Cambridge, UK: Cambridge University Press.

- Hansen, E.M., D.J. Goheen, E.S. Jules, and B. Ullian. 2000. Managing Port-Orford-cedar and the introduced pathogen *Phytophthora lateralis*. *Plant Disease* 84: 4-14.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K.Cromack, Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.
- Harmon, J.M., and J.F. Franklin. 1995. *Seed rain and seed bank of third- and fifth-order streams on the western slope of the Cascade Range*. USDA Forest Service, Pacific Northwest Research Station, Research Paper PNW-RP-480.
- Harrison S., J.H. Viers, and J.F. Quinn. 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. *Diversity and Distributions* 6: 153-161.
- Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management* 155: 81-95.
- Haskell, D.G. 2000. Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian Mountains. *Conservation Biology* 14: 57-63.
- Hawk, G.M. and D.B. Zobel, D.B. 1974. Forest succession on alluvial landforms of the McKenzie River Valley, Oregon. *Northwest Science* 48: 245-265.
- Hawkins, C.P., and J.R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62: 387-397.
- Hawkins, C.P., M.L. Murphy, and N.H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63: 1840-1856.
- Hawkins, C.P., M.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 1173-1185.
- Hayes, J.P. 2003. Habitat ecology and conservation of bats in western coniferous forests. In *Mammalian community dynamics: Management and conservation in the coniferous forests of western North America*, ed. C.J. Zabel and R.G. Anthony, 81-119. Cambridge, UK: Cambridge University Press.
- Hayes, J.P., and M.D. Adam. 1996. The influence of logging riparian areas on habitat utilization by bats in western Oregon. In *Bats and forests symposium*, ed. R.M.R. Barclay and R.M. Brigham, 228-237. Working paper 23/1996, Research Branch, Ministry of Forestry, British Columbia.
- Hayes, J.P., S.S. Chan, W.H. Emmingham, J.C. Tappeiner, L.D. Kellog, and J.D. Bailey. 1997. Wildlife response to thinning young forests in the Pacific Northwest. *Journal of Forestry* 95: 28-33.
- Hayes, J., and D. Waldien. 2001. Influence of coarse wood on small mammals in the Oregon Coast Range. In *Cooperative forest ecosystem 2001 annual research report*, 31-34. Corvallis, OR: Oregon State University.
- Hayes, J.P., and J.C. Hagar. 2002. Ecology and management of wildlife and their habitats in the Oregon Coast Range. In *Forest and stream management in the Oregon Coast Range*, ed. S.D. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner II, and G.E. Wells, 99-134. Corvallis, OR: Oregon State University Press.

- Hayes, J. P., J.M. Weikel, and M.P. Huso. 2003. Response of birds to thinning young Douglas-fir forests. *Ecological Applications* 13:1222-1232.
- Haynes, R.W., R.T. Graham, and T.M. Quigley, eds. 1996. *A framework for ecosystem management in the Interior Columbia Basin*. USDA Forest Service, General Technical Report. PNW-GTR-374.
- He, F., and H.J. Barclay. 2000. Long-term response of understory plant species to thinning and fertilization in a Douglas-fir plantation on southern Vancouver Island, British Columbia. *Canadian Journal of Forest Research* 30: 566-572.
- Healey, M.C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. In *Salmonid age at maturity*, ed. D.J. Meerburg, 39-52. *Canadian Special Publications on Fisheries and Aquatic Sciences* 89.
- Henderson, J.A. 1978. Plant succession on the *Alnus rubra/Rubus spectabilis* habitat type in western Oregon. *Northwest Science* 52: 156-167.
- Hershey, A.E., and G.A. Lamberti. 1998. Stream macroinvertebrate communities. In *River ecology and management: Lessons from the Pacific coastal ecoregion*, ed. R.J. Naiman and R.E. Bilby, 169-199. New York: Springer-Verlag.
- Hibbs, D.E., and Giordano, P.A. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. *Northwest Science* 70: 213-222.
- Hibbs, D.E., and S. Chan. 1997. Dynamics and silviculture of riparian vegetation. In *Annual report and bibliography: Coastal Oregon productivity enhancement program*, ed. J. Thomas, 43-47. Corvallis, OR.
- Hibbs, D.E., and Bower, A.L. 2001. Riparian forests in the Oregon Coast Range. *Forest Ecology and Management* 154: 201-213.
- Hicks, B.J., J.D. Hall, P.A. Bisson, and J.R. Sedell. 1991. Responses of salmonids to habitat changes. In *Influences of forest and rangeland management on salmonid fishes and their habitats*, American Fisheries Society Special Publication 19, ed. W. R. Meehan, 483-518. Bethesda, MD.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climate data. *Science* 105: 367-368.
- Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62: 447-502.
- Humes, M.L., J.P. Hayes, and M. Collopy. 1999. Activity of bats in thinned, unthinned, and old-growth forests in western Oregon. *Journal of Wildlife Management* 63: 553-561.
- Hunter, M.L. 1999. Biological diversity. In *Maintaining biodiversity in forest ecosystems*, ed. M.L. Hunter, 3-21. Cambridge, UK: Cambridge University Press.
- Hupp, C.R. 1986. Upstream variation in bottomland vegetation patterns, northwestern Virginia. *Bulletin of the Torrey Botanical Club* 113: 421-430.
- Huston, M.A. 1979. A general hypothesis of species diversity. *American Naturalist* 113: 81-101.
- . 1994. *Biological diversity: The coexistence of species on changing landscapes*. Cambridge, UK: Cambridge University Press.

- . 1999. Forest productivity and diversity: Using ecological theory and landscape models to guide sustainable forest management. In *North American Science Symposium: Toward a unified framework for inventorying and monitoring forest ecosystem resources*, C. Aguirre-Bravo and C.R. Franco, compilers, 329-341. USDA Forest Service RMRS-P-12.
- Ice, G. 2000. The use of active watershed management to achieve or accelerate the accomplishment of watershed goals. In *Watershed management 2000: Science and engineering technology for the new millennium*, ed. M. Flug and D. Frevert. Fort Collins, CO: American Society of Civil Engineers.
- Ice, G. 2004. History of innovative Best Management Practice development and its role in addressing water quality limited waterbodies. *Environmental Engineering* 130(6): 684-689.
- Imhof, J.G., J. Fitzgibbon, and W.K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1): 312-326.
- Isaac, L.A., and H.G. Hopkins. 1937. The forest soil of the Douglas fir region, and changes wrought upon it by logging and sash burning. *Ecology*: 18: 264-279.
- Johansson, M.E, C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* 7: 593-598.
- Johnson, A.C., D.N. Swanston, and K.E. McGee. 2000. Landslide initiation, runout, and deposition within clearcuts and old-growth forests of Alaska. *Journal of the American Water Resources Association* 36: 17-30.
- Johnson, S.L., and J.A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 57 (Supplement 2): 30-39.
- Johnson, S.L., F.J. Swanson, G.E. Grant, and S.M. Wondzell. 2000. Riparian forest disturbances by a mountain flood - The influence of floated wood. *Hydrological Processes* 14: 3031-3050.
- Jones, J.A. 2002. Hydrologic processes and peak discharge response to forest removal, regrowth, and roads in 10 small experimental basins, western Cascades, Oregon. *Water Resources Research* 36: 261-2642.
- Jones, J.A., and G.E. Grant. 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. *Water Resources Research* 32: 959-974.
- Jones, J.A., F.J. Swanson, B.C. Wemple, and K.U. Snyder. 2000. Effects of roads on hydrology, geomorphology, and disturbance patches in stream networks. *Conservation Biology* 14: 76-85.
- Jones, M.D., D.M. Durall, and J.W.G. Cairney. 2003. Ectomycorrhizal communities in young forest stands regenerating after clearcut logging. *New Phytologist* 157: 399-422.
- Jonsson, B.G. 1996a. Riparian bryophytes of the H.J. Andrews Experimental Forest in the Western Cascades, Oregon. *Bryologist* 99: 226-235.
- . 1996b. Riparian bryophyte vegetation in the Cascade mountain range, northwest U.S.A.: Patterns at different scales. *Canadian Journal of Botany* 75: 744-761.
- Jules, E.S., M.J. Kauffman, W.D. Ritts, and A.L. Carroll. 2002. Spread of an invasive pathogen over a variable landscape: A nonnative root rot on Port Orford cedar. *Ecology* 83: 3167-3181.

- Kalisz, P.J. and J.E. Powell. 2000. Effects of prescribed fire on soil invertebrates in upland forests on the Cumberland Plateau of Kentucky, USA. *Natural Areas Journal* 20: 336-341.
- Karr, J.K., J.J. Rhodes, G.W. Minshall, F.R. Hauer, R.L. Beschta, C.A. Frissell, and D.A. Perry. 2004. The effects of postfire salvage logging on aquatic ecosystems in the American West. *BioScience* 54: 1029-1033.
- Kauffman, J.B., R.L Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22: 12-24.
- Kauffman, J.B., M. Mahrt, L. A. Mahrt, and W.D. Edge. 2001. Wildlife and riparian habitats. In *Wildlife-habitat relationships in Oregon and Washington*, D.H. Johnson and T.A. O'Neil, managing directors, 361-388. Corvallis, OR: Oregon State University Press.
- Kelsey, K.A., and S.D. West. 1998. Riparian wildlife. In *River ecology and management*, ed. R.J. Naiman and R. E. Bilby, 235-258. New York: Springer-Verlag.
- Kerr, J.T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385: 252-254.
- Kinley, T.A., and N.J. Newhouse. 1997. Relationship of riparian reserve zone width to bird density and diversity in southeastern British Columbia. *Northwest Science* 71: 75-86.
- Klein, J.P., and A. Vanderpoorten. 1997. Bryophytic vegetation in riparian forests: their use in the ecological assessment of the connectivity between the Rhine and its floodplain (Alsace, France). *Global Ecology and Biogeography Letters* 6: 257-265.
- Klinka, K., V.J. Krajina, A. Ceska, and A.M. Scagel. 1995. *Indicator plants of coastal British Columbia*. Vancouver, BC: UBC Press.
- Knight, R.L. 1988. Relationships of birds of prey and riparian habitat in the Pacific Northwest: An overview. In *Streamside management: Riparian wildlife and forestry interactions*, ed. K.J. Raedeke, 79-91. University of Washington, Institute of Forest Resources Contribution No. 59.
- Knoph, F.L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. In *Riparian ecosystems and their management: Reconciling conflicting uses*, R.R. Johnson, C.D. Ziebell, D.R. Patten, P.F. Ffolliot, and R.H. Hamre, Technical Coordinators, 105-111. USDA Forest Service General Technical Report RM-GTR-120.
- Knutson, K.L., and V.L. Naef. 1997. *Management recommendations for Washington's priority habitats: Riparian*. Olympia, WA: Washington Department of Fish and Wildlife.
- Kohm, K.A., and J.F. Franklin, eds. 1997. *Creating a forestry for the 21st century*. Covelo, CA: Island Press.
- Kolodziejczyk, R.I., and J.S. Richardson. 2001. Linking riparian tree species composition to stream faunal diversity. NABS Annual Meeting, LaCrosse, WI.
- Korb, J.E., Johnson, N.C., and W. W. Covington. 2004. Slash pile burning effects on soil biotic and chemical properties and plant establishment: Recommendations for amelioration. *Restoration Ecology* 12: 52-62.
- Kovalchik, B.L., and L.A. Chitwood. 1990. Use of geomorphology in the classification of riparian plant associations in mountainous landscapes of central Oregon, U.S.A. *Forest Ecology and Management* 33/34: 405-418.

- Kranabetter, J.M., and J. Friesen. 2002. Ectomycorrhizal community structure on western hemlock (*Tsuga heterophylla*) seedlings transplanted from forests into openings. *Canadian Journal of Botany* 80: 861-868.
- Lach, D., P. List, B. Steel, and B. Schindler. 2003. Advocacy and credibility of ecological scientists in resource decision making: A regional study. *BioScience* 53: 170-178.
- Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman, and K.M.S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 196-208.
- Lantz, R.L. 1970. Fish population impacts. In *Proceedings of a symposium on forest land uses and stream environment*, ed. J.T. Krygies, and J. D. Hall, 246-248. Corvallis, OR: Oregon State University.
- Larson, G.L., and C.D. McIntire. 1993. Food habits of different phenotypes of threespine stickleback in Paxton Lake, British Columbia. *Transactions of the American Fisheries Society* 122: 543-549.
- Layton, P.A., S.T. Guynn, and D.C. Guynn. 2003. *Wildlife and biodiversity metrics in forest certification systems*. Technical Bulletin 857. Research Triangle Park, NC: National Council for Air and Stream Improvement, Inc.
- Ledwith, T. 1996a. The effects of buffer strip width on air temperature and relative humidity in a stream riparian zone. *Watershed Management Council Networker* 5. http://watershed.org/news/sum_96/buffer.html (accessed September 29, 2005).
- Ledwith, T. 1996b. The effects of buffer strip width on air temperature and relative humidity in a stream riparian zone. *Watershed Management Council Networker* 6: 6-7.
- Lee, D., J. Sedell, B. Rieman, R. Thurow, and J. Williams. 1997. Broad-scale assessment of aquatic species and habitats. Chapter 4 in *An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins*, T.M. Quigley, S.J. Arbelbide, technical eds. USDA Forest Service, General Technical Report PNW-GTR-405.
- Leopold L.B., M.G. Wolman, and J.P. Miller. 1964. *Fluvial processes in geomorphology*. New York: Dover Publications.
- Lesica, P., B. McCune, S.V. Cooper, and W.H. Hong. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. *Canadian Journal of Botany* 69: 1745-1755.
- Liang, S.Y., and Seagle, S.W. 2002. Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83: 212-227.
- Lindenmayer, D.B., and J.F. Franklin. 2002. *Conserving forest biodiversity*. Covelo, CA: Island Press.
- Lindroth, C.H. 1961-69. The ground-beetles of Canada and Alaska. *Opuscula Entomologica* Supplements 1-6:1-1192.
- Lock, P.A., and R.J. Naiman. 1998. Effects of stream size on bird community structure in coastal temperate forests of the Pacific Northwest, USA. *Journal of Biogeography* 25: 773-782.
- Loefering, J.P., and R.G. Anthony. 1999. Distribution, abundance, and habitat association of riparian-obligate and -associated birds in the Oregon Coast Range. *Northwest Science* 73: 168-185.

- Loft, E.R., J.W. Menke, and T.S. Burton. 1984. Seasonal movements and summer habitats of female black-tailed deer. *Journal of Wildlife Management* 48: 1317-1325.
- Longton, R.E. 1980. Physiological ecology of mosses. In *The mosses of North America*, ed. R.J. Taylor and A.E. Leviton, 77-113. Pacific Division, American Association for the Advancement of Science.
- Longton, R.E. 1992. The role of bryophytes and lichens in terrestrial ecosystems. *Bryophytes and lichens in a changing environment*, ed. J.W. Bates and A.M. Farmer. Oxford, UK: Clarendon Press.
- MacArthur, R. H., and J. MacArthur. 1961. On bird species diversity. *Ecology* 42: 594-598.
- Madson, S.L. 1997. Correlation between structural heterogeneity and arthropod biodiversity: implications for forest management of Pacific Northwest forests. M.S. thesis, Oregon State University, Corvallis, OR.
- Malanson, G.P. 1984. Intensity as the third factor of disturbance regime and its effect on species diversity. *Oikos* 43: 411-413.
- Marcot, B.G. 1997. Biodiversity of old forests of the west: a lesson from our elders. In *Creating a forestry for the 21st century*, ed. K. A. Kohm and J. F. Franklin, 87-102. Covelo, CA: Island Press.
- Marcot, B.G., L.K. Croft, J.F. Lehmkuhl, R.H. Naney, C.G. Niwa, W.R. Owen, and R.E. Sandquist. 1998. *Macroecology, paleoecology, and ecological integrity of terrestrial species and communities of the interior Columbia River Basin and portions of the Klamath and Great Basins*. USDA Forest Service General Technical Report PNW-GTR-410.
- Martin, K.J., and W.C. McComb. 2002. Small mammal habitat associations at patch and landscape scales in Oregon. *Forest Science* 48: 255-264.
- May, C.L., and R.E. Gresswell. 2003a. Processes and rates of sediment and wood accumulation in headwater streams of the central Oregon Coast Range. *Earth Surface Processes and Landforms* 28: 409-424.
- . 2003b. Large wood recruitment and redistribution in headwater streams in the southern Oregon Coast Range, U.S.A. *Canadian Journal of Forest Research* 33: 1352-1362.
- May, R.M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science* 186: 645-647.
- McAuliffe, J.R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65: 894-908.
- McComb, W.C., C.L. Chambers, and M. Newton. 1993. Small mammal and amphibian communities and habitat associations in red alder stands, central Oregon Coast Range. *Northwest Science* 67: 181-188.
- McComb, W.C., K. McGarigal, and R.G. Anthony. 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. *Northwest Science* 67: 7-15.
- McComb, W.C., T.A. Spies, and W.H. Emmingham. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. *Journal of Forestry* 91: 31-42.

- . 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. *Bryologist* 96: 405-411.
- . 2000. Lichen communities as indicators of forest health. *Bryologist* 103: 353-356.
- McCune, B., and W.J. Daly. 1994. Consumption and decomposition of lichen litter in a temperate coniferous rainforest. *Lichenologist* 26: 67-71.
- McCune, B., R. Rosentreter, J.M. Ponzetti, and D.C. Shaw. 2000. Epiphyte habitats in an old conifer forest in western Washington, U.S.A. *Bryologist* 103: 417-427.
- McCune, B., J. Hutchinson, and S. Berryman. 2002. Concentration of rare epiphytic lichens along large streams in a mountainous watershed in Oregon, U.S.A. *Bryologist* 105: 439-450.
- McElravy, E.P., G.A. Lambert, and V.H. Resh. 1989. Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society* 8: 51-63.
- McGarigal, K., and W.C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. *Journal of Wildlife Management* 56: 10-23.
- McGarigal, K., S. A. Cushman, and S. G. Stafford. 2000. *Multivariate statistics for wildlife and ecology research*. New York: Springer-Verlag.
- McIntire, C.D., and J.A. Colby. 1978. A hierarchical model of lotic ecosystems. *Ecological Monographs* 48: 167-190.
- McNabb, D.H., and F.J. Swanson. 1990. Effects of fire on soil erosion. In *Natural and prescribed fire in Pacific Northwest forests*, ed. J.D. Walstad, S.R. Radosevich, and D.V. Sandberg, 159-176. Corvallis, OR: Oregon State University Press.
- Medina, A.L., and C. Martin. 1988. Stream channel and vegetation changes in sections of McKnight Creek, New Mexico. *Great Basin Naturalist* 48: 378-381.
- Metter, D. E. 1966. Some temperature and salinity tolerances of *Ascaphus trui* Stejneger. [sic] *Journal of the Idaho Academy of Sciences* 4: 44-47.
- Meyer, C. L., and T.D. Sisk. 2001. Butterfly response to microclimatic conditions following ponderosa pine restoration. *Restoration Ecology* 9:453-461.
- Miller, T.E. 1982. Community diversity and interactions between size and frequency of disturbance. *American Naturalist* 120: 533-536.
- Minore, D., and H.G. Weatherly. 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. *New Forests* 8: 249-263.
- Minshall, G.W., K.W. Cummins, R.C. Petersen, C.E. Cushing, D.A. Bruns, J.R. Sedell, et al. 1985. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1045-1055.
- Moldenke, A.R. 1975. Niche specialization and species diversity along a California transect. *Oecologia* 21: 219-242.
- . 1976a. California pollination ecology and vegetation types. *Phytologia* 34: 305-361.
- . 1976b. Evolutionary history and diversity of the bee faunas of Chile and Pacific North America. *Wasmann Journal of Biology* 34: 147-178.

- . 1979a. Pollination ecology in the Sierra Nevada. *Phytologia* 42: 223-282.
- . 1979b. Pollination ecology as an assay of ecosystemic structure: Convergent evolution in California and Chile. *Phytologia* 42: 415-454.
- . 1979c. Host-plant coevolution and the diversity of bees in relation to the flora of North America. *Phytologia* 43: 357-419.
- . 1999. Soil-dwelling arthropods: their diversity and functional roles. In *Proceedings: Pacific Northwest forest and rangeland soil organism symposium*, ed. R.T. Meurisse, W.G. Ypsilantis, and C. Seybold. USDA Forest Service, General Technical Report PNW-GTR-461.
- Moldenke, A.R., and C. Ver Linden. 2002. *Literature synthesis and recommendations for general surveys for arthropods in soil, litter and coarse woody debris in the southern range of the northern spotted owl*. Report prepared for USDA Forest Service. <http://www.ent.orst.edu/moldenka/Conservation/survey.htm> (accessed October 3, 2005).
- Molina, R., D. Pilz, J. Smith, S. Dunham, T. Dreisbach, T. O'Dell, and M. Castellano. 2001. Conservation of forest fungi in the Pacific Northwest: An integrated ecosystem approach. In *Fungal conservation: Issues and solutions*, ed. D. Moore, M.M Nauta, S.E. Evans, and E. Rotheroe, 19-63. Cambridge, UK: Cambridge University Press.
- Montgomery, D.R. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association* 35: 397-410.
- Moran, V.C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology* 50: 153-164.
- Moring, J.R., and R.L. Lantz. 1975. *The Alsea watershed study: Effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon, Part I – Biological studies*. Fishery Research Report Number 9. Corvallis, OR: Oregon Department of Fish and Wildlife.
- Mouw, J.E.B., and P.A. Alaback. 2002. Putting floodplain hyperdiversity in a regional context: An assessment of terrestrial-floodplain connectivity in a montane environment. *Journal of Biogeography* 30: 87-103.
- Murphy, M.L., and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 137-145.
- Murphy, M.L., C.P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Transactions of the American Fisheries Society* 110: 469-478.
- Naiman, R.J. 1998. Biotic stream classification. In *River ecology and management: Lessons from the Pacific coastal ecoregion*, ed. R.J. Naiman and R.E. Bilby, 97-119. New York: Springer-Verlag.
- Naiman, R.J., T.J. Beechie, L.E. Benda, D.R. Berg, P.A. Bisson, L.H. MacDonald, M.D. O'Connor, P.L. Olson, and E.A. Steel. 1992. Fundamental elements of ecologically healthy watersheds in the Pacific Northwest Coastal Ecoregion. In *Watershed management: Balancing sustainability and environmental change*, ed. R. J. Naiman, 127-188. New York: Springer-Verlag.
- Naiman, R.J., and E.C. Anderson. 1997. Streams and rivers: Their physical and biological variability. In *The rain forests of home: Profile of a North American bioregion*, ed. P.K. Schoonmaker, B. Von Hagen, and E.L. Wolfe, 131-148. Washington, DC: Island Press.

- Naiman, R.J., K.L. Fetherston, S.J. McKay, and J. Chen. 1998. Riparian forests. In *River ecology and management*, ed. R.J. Naiman and R.E. Bilby, 289-318. New York: Springer-Verlag.
- Naiman, R.J., R.E. Bilby, and P.A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50: 996-1011.
- National Commission on Science for Sustainable Forestry (NCSSF). 2005. *Science, biodiversity, and sustainable forestry: A findings report of the National Commission on Science for Sustainable Forestry*. Washington, DC: National Commission on Science for Sustainable Forestry.
- Neal, F.D., and J.E. Borrecco. 1981. Distribution and relationship of mountain beaver to openings in sapling stands of Douglas-fir (*Pseudotsuga menziesii*). *Northwest Science* 55: 79-86.
- Neary, D.G., C.C. Klopatek, L.F. DeBano, and P.F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51-71.
- Neary, D.G., L.F. DeBano, and P.F. Ffolliott. 2000. Fire impacts on forest soils: A comparison to mechanical and chemical site preparation. In *Fire and forest ecology: Innovative silviculture and vegetation management*, ed. W.K. Moser and C.F. Moser, 85-94. Tall Timbers Ecology Conference Proceedings, No. 21. Tallahassee, FL: Tall Timbers Research Station.
- Neher, D.A., K.N. Easterling, D. Fiscus, and C.L. Campbell. 1998. Comparison of nematode communities in agricultural soils of North Carolina and Nebraska. *Ecological Applications* 8: 213-223.
- Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16: 4-21.
- Neitlich, P.N., and B. McCune. 1997. Hotspots of epiphytic lichen diversity in two young managed forests. *Conservation Biology* 11: 172-182.
- Newbold, J.D., D.C. Erman, and K.B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 1076-1085.
- Nickelson, T.E., M.F. Solazzi, S.L. Johnson, and J.D. Rodgers. 1992. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 790-794.
- Niemi, G.J., P. DeVore, N. Detenbeck, D. Taylor, A. Lima, J. Pastor, J.D. Yount, and R.J. Naiman. 1990. Overview of case studies on recovery of aquatic systems from disturbance. *Environmental Management* 14: 571-587.
- North, M., J. Trappe, and J.F. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. *Ecology* 78: 1543-1554.
- Northcote, T.G. 1997. Potamodromy in salmonidae--Living and moving in the fast lane. *North American Journal of Fisheries Management* 17: 1029-1045.
- Nussbaum, R.A., E.D. Brodie, Jr., and R.M. Storm. 1983. *Amphibians and reptiles of the Pacific Northwest*. Moscow, ID: University Press of Idaho.
- O'Connell, M.A., J.G. Hallett, S.D. West, K.A. Kelsey, D.A. Manuwal, and S.F. Pearson. 2000. *Effectiveness of riparian management zones in providing habitat for wildlife*. Final report to Timber, Fish and Wildlife Program (TFW-LWAG1-00-001), Washington Department of Natural

Resources. http://www.dnr.wa.gov/forestpractices/adaptivemanagement/cmer/publications/TFW_LWAG1_00_001.pdf (accessed September 29, 2005).

- O'Dell, T.E., J.F. Ammirati, and E.G. Schreiner. 1999. Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone. *Canadian Journal of Botany* 77: 1699-1711.
- Odion, D.C., and F.W. Davis. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecological Monographs* 70: 149-169.
- Odion, D.C., E.J. Frost, J.R. Strittholt, H. Jiang, D.A. DellaSala, and M.A. Moritz. 2004. Patterns of fire severity and forest conditions in the Klamath Mountains, Northwestern California, U.S.A. *Conservation Biology* 18: 927-936.
- Ohmann, J., and T. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* 68: 151-182.
- Olson, D.H., S.S. Chan, P. Cunningham, B. Hansen, A. Moldenke, R. Progar, P.S. Muir, B. McCune, A. Rosso, and E.B. Peterson. 2000a. Characterizing managed headwater forests - Integration of stream, riparian, and upslope habitats and species in western Oregon: Companion projects to the BLM density management studies. In *Proceedings of the Society of American Foresters 1999 national convention*, 539-540. SAF Publication 00-1, Bethesda, MD: Society of American Foresters.
- Olson, D.H., S.S. Chan, G. Weaver, P. Cunningham, A. Moldenke, R. Progar, P.S. Muir, B. McCune, A. Rosso, and E.B. Peterson. 2000b. Characterizing stream, riparian, upslope habitats and species in Oregon managed headwater forests. In *Riparian ecology and management in multi-land use watersheds. International conference of the American Water Resources Association*, ed. J. Wiggington, and R. Beschta, 83-88. AWRA Publication TPS-00-2, Middleburg, VA.: American Water Resources Association.
- Olson, D.H., J.C. Hagar, A.B. Carey, J.H. Cissel, and F.J. Swanson. 2000c. Wildlife communities in westside and high montane forest. In *Wildlife-habitat relationships in Oregon and Washington*, D.H. Johnson, and T.A. O'Neil, Managing Directors, 187-212. Corvallis, OR: Oregon State University Press.
- O'Neil, T.A., D.H. Johnson, C. Barrett, M. Trevithick, K.A. Bettinger, C. Kiilsgaard, M. Vander Heyden, E.L. Greda, D. Stinson, B.G. Marcot, P.J. Doran, S. Tank, and L. Wunder. 2001. Matrixes for wildlife-habitat relationships in Oregon and Washington. CD-ROM in *Wildlife-habitat relationships in Oregon and Washington*, D.H. Johnson, and T.A. O'Neil, Managing Directors. Corvallis OR: Oregon State University Press.
- Pabst, R.J., and T.A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. *Canadian Journal of Botany* 76: 298-315.
- . 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, U.S.A. *Canadian Journal of Forest Research* 29: 1557-1573.
- . 2001. Ten years of vegetation succession on a debris-flow deposit in Oregon. *Journal of the American Water Resources Association* 37: 1693-1708.
- Paine, R.T. 1980. Food webs: Linkage, interaction, strength, and community infrastructure. *Journal of Animal Ecology* 49: 667-685.

- Pankhurst, C., B. Doube, and V. Gupta, eds. 1997. *Biological Indicators of Soil Health*. New York: Oxford University Press.
- Pearson, S.F., and D.A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-fir forests. *Ecological Applications* 11: 840-853.
- Peck, J.E., and P.S. Muir. 2001. Estimating the biomass of harvestable epiphytic moss in central western Oregon. *Northwest Science* 75: 99-106.
- Perkins, T.E. 2000. The spatial distribution of beaver (*Castor canadensis*) impoundments and effects on plant community structure in the lower Alsea drainage of the Oregon Coast Range. M.S. thesis, Oregon State University, Corvallis, OR.
- Perry, D.A. 1994. *Forest ecosystems*. Baltimore, MD: Johns Hopkins University Press.
- Perry, D.A., R. Meurisse, B. Thomas, R. Miller, and J. Boyle, eds. 1989. *Maintaining the long-term productivity of Pacific Northwest forest ecosystems*. Portland, OR: Timber Press.
- Perry, D.A., and M.P. Amaranthus. 1997. Disturbance, recovery and stability. In *Creating a forestry for the 21st century*, ed. K.A. Kohm, and J.F. Franklin, 31-56. Covelo CA: Island Press.
- Pess, G.R., D.R. Montgomery, E.A. Steel, R.E. Bilby, B.E. Feist, and H.M. Greenberg. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. *Canadian Journal Fisheries and Aquatic Sciences* 59: 613-623.
- Peterson, G. D. 2002. Contagious disturbances, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5: 329-338.
- Petraitis, P.S., R.E. Latham, and R.A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *Quarterly Review of Biology* 64: 393-418.
- Piccolo, J.J., and M.S. Wipfli. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? *Canadian Journal of Fisheries and Aquatic Sciences* 59: 503-513.
- Pickett, S.T.A., and P.S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Orlando, FL: Academic Press.
- Pike, L.H., W.C. Denison, D.M. Tracy, M.A. Sherwood, and F.M. Rhoades. 1975. Floristic survey of the epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *Bryologist* 78: 389-402.
- Pilliod, D., R.B. Bury, E.J. Hyde, C.A. Pearl, and P.S. Corn. 2003. Fire and aquatic amphibians in North America. *Forest Ecology and Management* 178: 163-181.
- Pilz, D.P., and D.A. Perry. 1984. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. *Canadian Journal of Forest Research* 14: 94-100.
- Planty-Tabacchi, A.M., E. Tabacchi, R.J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10: 598-607.
- Poage, N.J. 1994. Comparison of stand development of a deciduous-dominated riparian forest and a coniferous-dominated riparian forest in the Oregon Coast Range. M.S. thesis, Oregon State University, Corvallis, OR.
- Poff, N.L., and J.V. Ward. 1990. Physical habitat template of lotic systems: Recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* 14: 629-645.

- Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76: 606-627.
- Poff, R.J. 1996. Effects of silvicultural practices and wildfire on productivity of forest soils. In *Sierra Nevada ecosystem project: Final report to Congress, Vol. II, Assessments and scientific basis for management options*, 473-489. Davis, CA: University of California, Centers for Water and Wildland Resources.
- Pollock, M.M., R.J. Naiman, and T.A. Hanley. 1998. Plant species richness in riparian wetlands – A test of biodiversity theory. *Ecology* 79: 94-105.
- Poole, G.C., C.A. Frissell, and S.C. Ralph. 1997. In-stream habitat unit classification: Inadequacies for monitoring and some consequences for management. *Journal of the American Water Resources Association* 33: 879-896.
- Porter, P.E., and W. R Meehan. 1987. *Seasonal species composition of invertebrates in several Oregon streams*. USDA Forest Service Research Paper PNW-RP-382.
- Postle, A., J. Majer, and D. Bell. 1991. A survey of selected soil and litter invertebrate species from the northern jarrah (*Eucalyptus marginata*) forest of western Australia, with particular reference to soil-type, stratum, seasonality and the conservation of forest fauna. In *Conservation of Australia's forest fauna*, ed. D. Lunney, 193-204. New South Wales, Australia: The Royal Zoological Society of New South Wales.
- Potter, K.M., F.W. Cabbage, G.B. Blank, and R.H. Schaberg. 2004. A watershed-scale model for predicting nonpoint pollution risk in North Carolina. *Environmental Management* 34(1):62-74.
- Progar, R., and A.R. Moldenke. 2002. Insect production from temporary and perennially flowing headwater streams in western Oregon. *Journal of Freshwater Ecology* 17: 391-407.
- Propst, D.L., J.A. Stefferud, and P.R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae*. *The Southwestern Naturalist* 37: 117-125.
- Rambo, T.R. 2001. Decaying logs and habitat heterogeneity: Implications for bryophyte diversity in western Oregon. *Northwest Science* 75: 270-277.
- Rambo, T.R., and P.S. Muir. 1998. Bryophyte species associations with coarse woody debris and stand ages in Oregon. *Bryologist* 101: 366-376.
- Rathcke, B., and E.S. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science* 65: 273-277.
- Reeves, G.H., F.H. Everest, and J.R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. *Transactions of the American Fisheries Society* 122: 309-317.
- Reeves, G.H., L.E. Benda, K.M. Burnett, P.A. Bisson, and J.R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17: 334-349.
- Reeves, G.H., P.A. Bisson, and J.M. Dambacher. 1998. Fish communities. In *River ecology and management: Lessons from the Pacific coastal ecoregion*, ed. R.J. Naiman and R.E. Bilby, 200-234. New York: Springer-Verlag.

- Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R.C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of North American Benthological Society* 7: 433-455.
- Richards, C., and G.W. Minshall. 1992. Spatial and temporal trends in stream macroinvertebrate communities: the influence of catchment disturbance. *Hydrobiologia* 241: 173-184.
- Richards, C., R.J. Haro, L.B. Johnson, and G.E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology* 37: 219-230.
- Rieman, B.E., and J. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transaction of the American Fisheries Society* 124: 285-296.
- Rieman, B.E., D.C. Lee, and R.F. Thurow. 1997. Distribution, status, and likely future trends of bull trout in the interior Columbia River basin and Klamath River basins. *North American Journal of Fisheries Management* 17: 1111-1125.
- Rieman, B.E., D.C. Lee, R.F. Thurow, P.F. Hessburg, and J.R. Sedell. 2000. Toward an integrated classification of ecosystems: Defining opportunities for managing fish and forest health. *Environmental Management* 25: 425-444.
- Rieman, B.E., D. Lee, D. Burns, R.E. Gresswell, M. Young, R. Stowell, J. Rinne, and P. Howell. 2003. Status of native fishes in the western United States and issues for fire and fuels management. *Forest Ecology and Management* 178: 197-211.
- Rinne, J.N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* 16: 653-658.
- Ritland, K., L.A. Dupuis, F.L. Bunnell, W.L.Y. Hung, and J.E. Carlson. 2000. Phylogeography of the tailed frog (*Ascaphus truei*) in British Columbia. *Canadian Journal of Zoology* 78: 1749-1758.
- Roberts, M.R., and F.S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Applications* 5: 969-977.
- Robison, G., K. Mills, J. Paul, L. Dent, and A. Skaugset. 1999. *Oregon Department of Forestry storm impacts and landslides of 1996: Final report*. Oregon Department of Forestry Forest Practices Monitoring Program.
- Robinson, C.T., and G.W. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in canopy cover and season. *Journal of North American Benthological Society* 5: 237-248.
- Roxburgh, S.H., K. Shea, and J.B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85: 359-371.
- Ruchty, A., A.L. Rosso, and B. McCune. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. *Bryologist* 104: 274-281.
- Rundio, D.E., and D.H. Olson. 2001. Predator-prey relations between southern torrent salamanders (*Rhyacotriton variegatus*) and Pacific giant salamander (*Dicamptodon tenebrosus*) larvae. *Journal of Herpetology* 35: 133-136.
- Runkle, J. R. 1985. Disturbance regimes in temperate forests. In *The ecology of natural disturbance and patch dynamics*, ed. S.T.A. Pickett and P.S. White, 17-34. New York: Academic Press.

- Runyon, J., R.H. Waring, S.N. Goward, and J.M. Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecological Applications* 4: 226-237.
- Russell, W.H., and Jones, C. 2001. The effects of timber harvesting on the structure and composition of adjacent old-growth coast redwood forest, California, USA. *Landscape Ecology* 16: 731-741.
- Rykiel, E. J. 1985. Toward a definition of ecological disturbance. *Australian Journal of Ecology* 10: 361-365.
- Rykiel, E.J. 2001. Scientific objectivity, value systems, and policymaking. *BioScience* 51: 433-436.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: A hierarchical analysis. *Ecological Applications* 9: 135-151.
- Sakai, T. T. Hiroshi, W. Suzuki, H. Nomuya, T. Kanazashi, S. Iida, and T. Nakashizuka. 1999. Riparian disturbance and community structure of a *Quercus-Ulmus* forest in central Japan. *Plant Ecology* 140: 99-109.
- Sarr, D. 2002. Riparian livestock exclosure research in the western United States: a critique and some recommendations. *Environmental Management* 30: 516-526.
- . 2005. Hierarchical controls on woody riparian vegetation: distribution, diversity, and tree regeneration in four western Oregon watersheds. Ph.D. diss., Oregon State University, Corvallis, OR.
- Sarr, D.A., D.E. Hibbs, and M.A. Huston. 2005. A hierarchical perspective of plant diversity. *Quarterly Review of Biology* 80:187-212.
- Schaffer, W.H., and P.F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology* 56:577-590.
- Schofield, W.B. 1984. Bryogeography of the Pacific coast of North America. *Journal of the Hattori Botanical Laboratory* 55:35-43.
- Schofield, W.B. 1988. Bryogeography and the bryophytic characterization of biogeoclimatic zones of British Columbia, Canada. *Canadian Journal of Botany* 66: 2673-2686.
- Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *Forest Science* 34: 960-979.
- Schowalter, T., E. Hansen, R. Molina, and Y. Zhang. 1997. Integrating the ecological roles of phytophagous insects, plant pathogens, and mycorrhizae in managed forests. In *Creating a forestry for the 21st century*, ed. K.A. Kohm and J.F. Franklin, 171-190. Covelo, CA: Island Press.
- Sedell, J.R., and R.L. Beschta. 1991. Bringing back the “bio” in bioengineering. *American Fisheries Society Symposium* 10: 160–175.
- Seidman, V.M., and C.J. Zabel. 2001. Bat activity along intermittent streams in northeastern California. *Journal of Mammalogy* 82: 738-747.
- Shea, K., S.H. Roxburgh, and E.S.J. Rauschert. 2004. From pattern to process: Coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* 7: 491–508.

- Shirato, L., ed. 1991. *Judging the validity of information sources: Teaching critical analysis in bibliographic instruction*. Ann Arbor, MI: Pierian Press.
- Sillett, S.C., and M.N. Goslin. 1999. Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest. *Canadian Journal of Forest Research*. 29: 1204-1215.
- Sillett, S.C., B. McCune, J.E. Peck, T.R. Rambo, and A. Ruchty. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. *Ecological Applications* 10: 789-799.
- Simard, S.W., D.A. Perry, M.D. Jones, D.D. Myrold, D. M. Durrall, and R. Molina. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 338:579-581.
- Skinner, C.N. 2003. A tree-ring based fire history of riparian reserves in the Klamath Mountains. In *Proceedings of the conference on riparian habitat and floodplains*, ed. P.M. Faber, 16-19. Sacramento, CA: Riparian Habitat Joint Venture.
- Smith, G.R. 1981. Late cenozoic freshwater fishes of North America. *Annual Review of Ecology and Systematics* 112: 163-193.
- Smith, J.P., R.E. Gresswell, and J.P. Hayes. 1997. *A research problem analysis in support of the Cooperative Forest Ecosystem Research (CFER) program*. Final Report on Contract H952A1-0101-25. Corvallis, OR: Oregon State University.
- Smock, L.A. 1996. Macroinvertebrate movements: Drift, colonization, and emergence. In *Methods in stream ecology*, ed. F.R. Hauer and G.A. Lamberti, 371-390. San Diego, CA: Academic Press.
- Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: The nonequilibrium maintenance of species diversity. *Ecology* 60: 1225-1239.
- Spies, T.A., J.F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20: 649-658.
- Spies, T.P., and M.G. Turner. 1999. Dynamic forest mosaics. In *Maintaining biodiversity in forest ecosystems*, ed. M.L. Hunter, Jr., 95-160. New York: Cambridge University Press.
- Spira, T.P. 2001. Plant-pollinator interactions: A threatened mutualism with implications for the ecology and management of rare plants. *Northwest Areas Journal* 21: 71-81.
- Springett, B.P. 1976. The effect of planting *Pinus pinaster* Ait. on populations of soil microarthropods and on litter decomposition at Gngangara, Western Australia. *Australian Journal of Ecology* 1: 83-87.
- Stanford, J.A., and J.V. Ward. 1992. Aquatic resources in large catchments. In *Watershed management: Balancing sustainability and environmental change*, ed. R.J. Naiman, 91-124. New York: Springer-Verlag.
- Steel, E.A., R.J. Naiman, and S.D. West. 1999. Use of woody debris piles by birds and small mammals in a riparian corridor. *Northwest Science* 73: 19-26.
- Steinblums, I.J., H.A. Froehlich, and J.K. Lyons. 1984. Designing stable buffer strips for stream protection. *Journal of Forestry* 81: 49-52.
- Stewart, G.H. 1988. The influence of canopy cover on understory development in forests of the western Cascade Range, Oregon, USA. *Vegetatio* 76: 79-88.

- Stinton, D.S., J.A. Jones, J.L. Ohmann, and F.J. Swanson. 2000. Windthrow disturbance, forest composition, and structure in the Bull Run Basin, Oregon. *Ecology* 81: 2539-2556.
- Stohlgren, T.J., G.W. Chong, M.A. Kalkhan, and L.D. Schell. 1997. Multi-scale sampling of plant diversity: effects of minimum mapping unit size. *Ecological Applications* 7: 1064-1074.
- Stork, N.E. 1990. *The role of ground beetles in ecological and environmental studies*. Andover, MD: Intercept Press.
- Sullivan, K., T.E. Lisle, C.A. Dolloff, G.E. Grant, and L.M. Reid. 1987. Stream channels: The link between forests and fishes. In *Streamside management: Forestry and fishery interactions*, ed. E.O. Salo and T.W. Cundy, 39-97. Institute of Forest Resources Contribution 57. University of Washington, College of Forest Resources, Seattle, WA.
- Suzuki, N. 1992. Habitat classification and characteristics of small mammal and amphibian communities in beaver-pond habitats of the Oregon Coast Range. M.S. thesis, Oregon State University, Corvallis, OR.
- Suzuki, N., and W.C. McComb. 1998. Habitat classification models for beaver (*Castor canadensis*) in streams of the central Oregon Coast Range. *Northwest Science* 72: 102-110.
- Swanson, F.J. 1981. Fire and geomorphic processes. In *Proceedings of the conference on fire regimes and ecosystems*, ed. H.A. Mooney, 401-420. General Technical Report WO-GTR-26. Washington, DC: USDA Forest Service.
- Swanson, F.J., S.V. Gregory, J.R. Sedell, and A.G. Campbell. 1982. Land-water interactions: The riparian zone. In *Analysis of coniferous forest ecosystems in the Western United States*, ed. R.L. Edmonds, 267-291. US/IBP Synthesis Series 14. Stroudsburg, PA: Hutchinson Ross Publishing Co.
- Swanson, F.J., L.E. Benda, S.H. Duncan, G.E. Grant; W.F. Megahan; L.M. Reid, and R.R. Ziemer. 1987. Mass failures and other processes of sediment production in Pacific Northwest forest landscapes. In *Streamside management: Forestry and fishery interactions*, ed. E.O. Salo and T.W. Cundy, 9-38. Institute of Forest Resources Contribution 57. University of Washington, College of Forest Resources, Seattle, WA.
- Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38: 92-98.
- Swanson, F.J., J.L. Clayton, W.F. Megahan, and G. Bush. 1989. Erosional processes and long-term site productivity. In *Maintaining the long-term productivity of Pacific Northwest forest ecosystems*, ed. D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R.F. Powers, 67-81. Portland, OR: Timber Press.
- Tabacchi, E., A.M. Planty-Tabacchi, M.J. Salinas, and H. Decamps. 1996. Landscape structure and diversity in riparian plant communities: A longitudinal comparative study. *Regulated Rivers: Research and Management* 12: 367-390.
- Tan, B.C., and Pocs T. 2000. Bryogeography and conservation of bryophytes. In *Bryophyte biology*, ed. A.J. Shaw and B. Goffinet, 403-448. Cambridge, UK: Cambridge University Press.
- Tappeiner, J.C., D.H. Olson, and C.R. Thompson. 2000. Density management studies of western Oregon. In *Proceedings of the Society of American Foresters 1999 national convention*, 556-557. SAF Publication 00-1. Bethesda, MD: Society of American Foresters.

- Tappeiner, J.C., W.H. Emmingham, and D.E. Hibbs. 2002. Silviculture of the Oregon Coast Range forests. In *Forest and stream management in the Oregon Coast Range*, ed. S.H. Hobbs, J.P. Hayes, R.L. Johnson, G.H. Reeves, T.A. Spies, J.C. Tappeiner II, and G.E. Wells, 172-190. Corvallis, OR: Oregon State University Press.
- Thiele, H.U. 1977. *Carabid beetles in their environments*. New York: Springer-Verlag.
- Thomas, S.C., C.B. Halpern, D.A. Falk, D.A. Liguori, and K.A. Austin. 1999. Plant diversity in managed forests: Understory responses to thinning and fertilization. *Ecological Applications* 9: 864-879.
- Thompson, I., and P. Angelstam. 1999. Special species. In *Maintaining biodiversity in forest ecosystems*, ed. M. Hunter, 434-459. Cambridge, UK: Cambridge University Press.
- Thurow, R.F., D.C. Lee, and B.E. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia Basin and portions of the Klamath River and Great Basins. *North American Journal of Fisheries Management* 17: 1094-1110.
- Tilman, D. 1996. Biodiversity: Population versus ecosystem stability. *Ecology* 77: 350-63.
- Triska, F.J., J.R. Sedell, and S.V. Gregory. 1982. Coniferous forest streams. In *Analysis of coniferous forest ecosystems in the western United States*, ed. R. L. Edmonds, 292-332. US/IBP Synthesis Series 14. Stroudsburg, PA: Hutchinson Ross Publishing Co.
- Trombulak, S.C., and Frissell, C.A. 2000. Review of the ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14: 18-30.
- Trotter, P.C. 1989. Coastal cutthroat trout: A life history compendium. *Transaction of the American Fisheries Society* 118: 463-473.
- Turner, M.G. and W.H. Romme. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecology* 9: 59-77.
- USDA Forest Service and USDI Bureau of Land Management. 1994. *Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl and standards and guidelines of management of habitat for late-successional and old-growth species within the range of the Northern Spotted Owl*. Washington, DC: USDA Forest Service and USDI Bureau of Land Management.
- Van Sickle, J., and S.V. Gregory. 1990. Modeling inputs of large woody debris to streams from falling trees. *Canadian Journal of Forest Research* 20: 1593-1601.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Vesely, D.G., and W.C. McComb. 2002. Salamander abundance and amphibian species richness in riparian buffer strips in the Oregon Coast Range. *Forest Science* 48: 291-297.
- Vitousek, P.M., and D.U. Hooper. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In *Ecosystem function of biodiversity*, ed. E. D. Schulze and H.A. Mooney, 3-14. Heidelberg, Germany: Springer-Verlag.
- Wahbe, T.R. 1996. Tailed frogs (*Ascaphus truei* Stejneger) in natural and managed coastal temperate rainforests of southwestern British Columbia, Canada. Masters thesis, University of British Columbia, Vancouver, B.C.

- Wahbe, T.R., F.L. Bunnell, and R.B. Bury. 2000. Defining wildlife habitat areas for tailed frogs. In *Proceedings of the biology and management of species and habitats at risk, volume two*, ed. L.M. Darling, 489-495. British Columbia Ministry of Environment, Lands, and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C.
- Waldien, D.L., and J.P. Hayes. 2001. Activity areas of female long-eared myotis in coniferous forests in western Oregon. *Northwest Science* 75: 307-314.
- Wallace, J.B., and N.H. Anderson. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. In *An introduction to the aquatic insects of North America*, 3rd edition, ed. R.W. Merritt and K.W. Cummins, 41-73. Dubuque, IA: Kendall/Hunt.
- Wallace, R.L., and L.V. Diller. 1998. Length of the larval cycle of *Ascaphus truei* in coastal streams of the redwood region, northern California. *Journal of Herpetology* 32: 404-409.
- Waring, R.H. 1969. Forest plants of the eastern Siskiyou: Their environmental and vegetational distribution. *Northwest Science* 43:1-17.
- Waring, R.H., and J. Major. 1964. Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light and temperature. *Ecological Monographs* 34:167-215.
- Waring, R.H., N.C. Coops, J.L. Ohmann, and D.A. Sarr. 2002. Interpreting woody plant richness from seasonal ratios of photosynthesis. *Ecology* 83: 2964-2970.
- Warner, R.R., and P.L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. *American Naturalist* 125:769-787.
- Waterhouse, F.L. 1998. Habitat of winter wrens in riparian and upland areas of coastal forests. M.S. thesis, Simon Fraser University, Burnaby, B.C.
- Watson, G., and T.W. Hillman. 1997. Factors affecting the distribution and abundance of bull trout: An investigation at hierarchical scales. *North American Journal of Fisheries Management* 17: 237-252.
- Welsh, H.H. 1990. Relictual amphibians and old-growth forests. *Conservation Biology* 4: 309-319.
- Welsh, H.H., and A.J. Lind. 1991. The structure of the herpetofaunal assemblage in the Douglas-fir hardwoods forests of northwestern California and southwestern Oregon. In *Wildlife and vegetation of unmanaged Douglas-fir forests*, L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff, Technical Coordinators, 394-413. USDA Forest Service, General Technical Report PNW-GTR-285.
- . 1996. Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in northwestern California. *Journal of Herpetology* 30: 385-398.
- . 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou Region of California and Oregon. *Journal of Wildlife Management* 66: 581-602.
- Welsh, H.H., A.J. Lind, L.A. Ollivier, G.R. Hodgson, and N.E. Karraker. 1998. Comments on the PALCO HCP/SYP and EIS/EIR with regard to the maintenance of riparian, aquatic, and late seral ecosystems and their associated amphibian and reptile species. USDA Forest Service, Redwood Sciences Lab, unpublished report. <http://www.fs.fed.us/psw/rsl/projects/wild/welsh/plhcp/plhcp.html> (accessed September 29, 2005).

- Wert, S. and B.R. Thomas. 1981. Effects of skid roads on diameter, height, and volume growth in Douglas-fir. *Soil Science Society of America Journal* 45: 629-632.
- West, S.D. 2000a. Westside small mammal surveys. In *Effectiveness of riparian management zones in providing habitat for wildlife*, ed. M.A. O'Connell, J.G. Hallett, S.D. West, K.A. Kelsey, D.A. Manuwal, and S.F. Pearson, pp. 10-1–11-60. Final report to Timber, Fish, and Wildlife Program. TFW-LWAG1-00-001. Olympia, WA: Washington Department of Natural Resources.
- . 2000b. Westside bat surveys. In *Effectiveness of riparian management zones in providing habitat for wildlife*, ed. M.A. O'Connell, J.G. Hallett, S.D. West, K.A. Kelsey, D.A. Manuwal, and S.F. Pearson, pp. 12-1–12-24. Final report to Timber, Fish, and Wildlife Program. TFW-LWAG1-00-001. Olympia, WA: Washington Department of Natural Resources.
- Westman, W.E. 1990. Biodiversity: Unresolved policy issues and questions. *BioScience* 40: 26-33.
- White, P.S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399-450.
- White, P.S., and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. In *The ecology of natural disturbance and patch dynamics*, ed. S.T.A. Pickett and P.S. White, 3-13. Orlando, FL: Academic Press.
- Whitlock C.W. 2004. Forests, fires, and climate. *Nature* 432: 28-29.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.
- . 1975. *Communities and ecosystems*. New York: MacMillan.
- Wikars, L.O., and J. Schimmel. 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *Forest Ecology and Management* 141: 189-200.
- Wiley, M.J., S.L. Kohler, and P.W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: Lessons from Michigan trout streams. *Freshwater Biology* 37: 133-148
- Wilkins, R.N., and N.P. Peterson. 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. *Forest Ecology and Management* 139: 79-91.
- Williams, J.A., and W. Nehlsen. 1997. Status and trends of anadromous salmonids in the coastal zone with special reference to sea-run cutthroat trout. In *Sea-run cutthroat trout: Biology, management, and future conservation*, ed. J.D. Hall, P.A. Bisson, and R.E. Gresswell, 37-42. Corvallis, OR: Oregon Chapter, American Fisheries Society.
- Wilson, E.O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1: 344-346.
- Wilzbach, M.A., Harvey, B.C., White, J.L., and Nakamoto, R.J. 2005. Effects of riparian canopy openings and salmon carcass addition on abundance and growth of resident salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 62(1): 58-67.
- Wimberly, M.C., and T.A. Spies. 2001. Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. *Ecology* 82: 1443-1459.

- Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: Contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1259-1269.
- Wipfli, M.S., and D.P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: Implications for downstream salmonid production. *Freshwater Biology* 47: 957-969.
- Wofford, J.E.B., R.E. Gresswell, and M.A. Banks. 2005. Factors influencing within-watershed genetic variation of coastal cutthroat trout. *Ecological Applications* 15: 628-637.
- Wright, J.P., C.G. Jones, and A.S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132: 96-101.
- Young, K.A. 2000. Riparian zone management in the Pacific Northwest: Who's cutting what? *Environmental Management* 26: 131-144.
- Young, M.K., ed. 1995. *Conservation assessment for inland cutthroat trout*. USDA General Technical Report RM-GTR-256, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Yount, J.D., and G.J. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance-a narrative review of case studies. *Environmental Management* 14: 547-569.
- Zabel, C.J., and J.R. Waters. 1997. Food preferences of captive northern flying squirrels from the Lassen National Forest in northeastern California. *Northwest Science* 71: 103-107.
- Zobel, D.B., A. McKee, and G.M. Hawk. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs* 46: 135-156.
- Zobel, D.B., L.F. Roth, and G.M. Hawk. 1985. *Ecology, pathology, and management of Port-Orford-cedar (Chamaecyparis lawsoniana)*. USDA Forest Service, General Technical Report PNW-184.

APPENDIX A

FOREST ZONES IN THE PACIFIC NORTHWEST

Table A1 describes general riparian and associated upland vegetation in forestlands and how it varies across the study area. Included is the Willamette Valley, much of which is not forested, but which supports plantations in and next to riparian areas. Descriptions are based on Franklin and Dyrness (1973), with supplemental information for California based on Barbour and Major (1977). Herbaceous understory species and non-vascular plants are too numerous to detail here, but are described in the above treatments.

Table A1 Summary of Riparian and Associated Upslope Vegetation (Excluding Lichens) in Forested Regions of the Pacific Northwest Where Private Lands Are Predominantly Located

Regional Vegetation Zone	Distribution	Dominant Riparian Trees*	Riparian Understory**	Upland Vegetation***
1. West of Cascade Crest, Excluding SW Oregon and NW California				
Sitka Spruce (<i>Picea sitchensis</i>) zone	Wet coastal strip from Alaska to N. Calif.	<i>Picea sitchensis</i> , <i>Tsuga heterophylla</i> , <i>Thuja plicata</i> <i>Pseudotsuga menziesii</i> ¹ , <i>Alnus rubra</i> ¹ , <i>Acer macrophyllum</i> ² , <i>Populus trichocarpa</i> ^{1,2}	Often well-developed, with woody species: <i>Rubus spectabilis</i> ¹ , <i>Vaccinium</i> spp., <i>Acer circinatum</i> , ferns, <i>Polystichum munitum</i> , and many forbs. Exceptional moss and liverwort abundance and diversity, many as epiphytes	Tree and shrub strata similar to riparian areas, but with much less hardwood (<i>Alnus</i> , <i>Acer</i>) cover.
Western Hemlock (<i>Tsuga heterophylla</i>) zone, coast ranges	Extensive at relatively low elevations (0-1200m) in Western Cascades and Coast Ranges of Washington, and Oregon.	<i>Alnus rubra</i> ¹ , <i>Acer macrophyllum</i> <i>Fraxinus latifolia</i> ² , <i>Pseudotsuga menziesii</i> ¹ , <i>Tsuga heterophylla</i> , <i>Thuja plicata</i> . <i>Chamaecyparis lawsoniana</i> ³ , <i>Populus trichocarpa</i> ^{1,2}	Well-developed under hardwood overstory, with woody species (<i>Rubus spectabilis</i> ^{1,4} , <i>Acer circinatum</i> , <i>Taxus brevifolia</i> , and ferns (<i>Polystichum munitum</i>). Many forbs. Exceptional moss and liver-wort abundance and diversity.	Tree and shrub strata similar to riparian areas. Less hardwood and understory cover, but <i>Alnus rubra</i> often follows stand-replacing fire or logging.
Western Hemlock (<i>Tsuga heterophylla</i>) zone, Cascades	Extensive at relatively low elevations (<1200 m) in western Cascades north of Rogue River.	<i>Pseudotsuga menziesii</i> ¹ , <i>Tsuga heterophylla</i> , <i>Thuja plicata</i> , <i>Alnus rubra</i> , ^{1,2} <i>Acer macrophyllum</i> , <i>Populus trichocarpa</i> ² , <i>Fraxinus latifolia</i> ²	With conifer dominance, not as well-developed as in coast ranges. Woody species (<i>Acer circinatum</i> , <i>Taxus brevifolia</i> , ferns (<i>Polystichum munitum</i>), and many forbs present. Abundant mosses and liverworts.	Less hardwood and understory cover, <i>Alnus rubra</i> absent.
Subalpine (<i>Abies amabilis</i>) zone	East side of Olympic Mts. and west slopes Of Cascades south to Central Oregon. At 600-1500 m. depending on latitude.	<i>Abies amabilis</i> , <i>Tsuga heterophylla</i> , <i>Picea engelmannii</i> , <i>Pseudotsuga menziesii</i> ¹ , <i>Populus trichocarpa</i> ²	Scattered woody species: <i>Oplomanax horridum</i> , <i>Vaccinium</i> spp. Herb-rich understory (e.g., <i>Tiarella</i> , <i>Smilacina</i> , <i>Clintonia</i> , and ferns). Mosses and liverwort common.	Tree and shrub strata similar to riparian areas. Less hardwood and understory cover.
Willamette Valley	Western Oregon	<i>Populus trichocarpa</i> ^{1,2} , <i>Fraxinus latifolia</i> , <i>Salix</i> spp. ^{1,2} , <i>Acer macrophyllum</i> , <i>Alnus rubra</i> ^{1,2} , <i>Quercus garryana</i> , <i>Pinus ponderosa</i> ¹ , <i>Abies grandis</i>	Varies from sparse to lush. <i>Salix</i> spp. ² , <i>Carex</i> spp. Mosses and liverworts common.	Mainly grasslands, and oak (<i>Quercus garryana</i>) woodlands.

(Continued on next page. See notes at end of table.)

Table A1 Continued

Regional Vegetation Zone	Distribution	Dominant Riparian Trees*	Riparian Understory**	Upland Vegetation***
2. SW Oregon and NW California				
Redwood (<i>Sequoia sempervirens</i>)	Near coast in Northern California and Extreme Southwest Oregon.	<i>Sequoia sempervirens</i> ¹ , <i>Tsuga heterophylla</i> , <i>Umbellularia californica</i> , <i>Acer macrophyllum</i> , ^{1,2} <i>Populus trichocarpa</i> ² , <i>Alnus</i> spp.	Often not well developed. <i>Polystichum munitum</i> , <i>Oxalis oregana</i> , <i>Woodwardia fimbriata</i> and other ferns and perennial forbs. Considerable moss and liverwort abundance.	Similar to riparian, but lower tree layer dominated by <i>Lithocarpus densiflorus</i> and <i>Arbutus menziesii</i> ⁵ .
Mixed evergreen <i>Pseudotsuga</i> / Sclerophyll zone	700-1500 m in Klamath Mountain Ranges. Widespread away from coast.	<i>Alnus</i> spp. ^{1,2} , <i>Fraxinus latifolia</i> ² , <i>Chamaecyparis lawsoniana</i> ⁶ , <i>Populus trichocarpa</i> ² , <i>Acer macrophyllum</i> ² , <i>Pseudotsuga menziesii</i> ¹	Relatively well developed and rich in woody species (<i>Acer circinatum</i> , <i>Rubus</i> spp., <i>Corylus cornuta</i> , <i>Rosa gymnocarpa</i> , <i>Physocarpus capitatus</i>) and ferns (<i>Polystichum munitum</i>). Scattered herbs, mosses, and liverworts.	Much <i>Pseudotsuga douglasii</i> , and <i>Abies concolor</i> , with lower tree layer dominated by <i>Lithocarpus densiflorus</i> and <i>Arbutus menziesii</i> ⁵ .
Mixed Conifer (<i>Pseudotsuga menziesii</i>) zone. (Upper elevation limit can be distinguished as the <i>Abies concolor</i> (zone).	700-2000 m, mainly in southern Cascades, but also found in the eastern Klamath Mountain Ranges.	<i>Alnus</i> spp. ^{1,2} , <i>Fraxinus latifolia</i> ² , <i>Populus trichocarpa</i> ² , <i>Acer macrophyllum</i> ² , <i>Abies concolor</i> , <i>Taxus brevifolia</i> , <i>Populus tremuloides</i> , <i>Tsuga heterophylla</i> ⁷ , <i>Pseudotsuga menziesii</i> ¹ , <i>Thuja plicata</i> ⁷	Well developed and relatively rich in woody species ⁸ (<i>Acer circinatum</i> , <i>Rubus</i> spp., <i>Corylus cornuta</i> , <i>Rosa gymnocarpa</i> , <i>Physocarpus capitatus</i>) and ferns (<i>Polystichum munitum</i>). Scattered herbs, mosses, and liverworts.	Much <i>Pseudotsuga menziesii</i> , <i>Abies Concolor</i> , with scattered <i>Pinus</i> spp. ⁹ and <i>Calocedrus decurrens</i> . Sub canopy of <i>Arbutus menziesii</i> and <i>Castanopsis chrysophylla</i> ⁵ . Fairly sparse understory.
3. Eastern Cascades				
Grand/white fir (<i>Abies grandis</i> / <i>Concolor</i>) zone	1,000-2,000 m. Extensive in Oregon, less common northward.	<i>Abies grandis/concolor</i> , <i>Populus tremuloides</i> , <i>Pinus contorta</i> .	Scattered woody species (<i>Salix</i> spp., <i>Vaccinium</i> spp., <i>Ribes</i> spp. and <i>Symphoricarpos albus</i> . Non forest, mountain meadow vegetation of grasses and sedges common. Scattered herbs, mosses, and liverworts.	Wide variety of conifers Scattered with <i>Abies</i> , Most common are <i>Pinus ponderosa</i> , <i>Pinus contorta</i> , <i>Larix occidentalis</i> and <i>Pseudotsuga menziesii</i> .

(Continued on next page. See notes at end of table.)

Table A1 Continued

Regional Vegetation Zone	Distribution	Dominant Riparian Trees*	Riparian Understory**	Upland Vegetation***
3. Eastern Cascades (cont'd)				
Western hemlock (<i>Tsuga heterophylla</i>) zone	Mainly in Washington and British Columbia at 800-1200m. Uncommon southward.	As described for Western Hemlock zone above, but <i>Thuja plicata</i> more common, and <i>Populus tremuloides</i> present.	As described for Western Hemlock zone above.	As described for Western Hemlock zone above, but <i>Thuja plicata</i> and <i>Pinus monticola</i> more common.
Eastside Pine (<i>Pinus ponderosa</i>)	Entire east Cascades in a 15-30 km wide band, 600-1200m elevation in the north and 900-1500 (2000)m in the south.	<i>Pinus ponderosa</i> ¹ , <i>Populus tremuloides</i> , <i>Pseudotsuga menziesii</i> ¹⁰ , <i>Abies grandis/concolor</i> ¹⁰ .	Well developed and relatively rich in woody species ⁸ . <i>Physocarpus malvaceus</i> , <i>Symphoricarpos albus</i> , <i>Holodiscus discolor</i> , <i>Ceanothus sanguineus</i> , <i>Ribes</i> spp. <i>Purshia tridentata</i> , perennial grasses, sedge (<i>Carex</i>) rushes (<i>Juncus</i>) and forbs.	Open <i>Pinus ponderosa</i> forest/ woodland with advanced <i>Abies</i> and <i>Pseudotsuga</i> regeneration. Understory of more drought adapted shrubs (<i>Artemisia</i> and bunch grasses (<i>Stipa</i> , <i>Agropyron</i>))

* In general order of dominance.

** Hydrophytic species such as willows (*Salix* spp.), sedges (*Carex* spp.), ferns (*Adiantum*, *Blechnum*), mosses and liverworts occur in all zones.

*** Compared to riparian areas within each zone. Hydrophytic vascular plant species described above (single asterisk) generally absent from upslope areas throughout the region.

¹ Shade intolerant, and consequently, regeneration into canopy occurs with opening of forest canopy through gap, fire, fluvial, etc. disturbance.

² Primarily or entirely found in riparian areas within the regional vegetation type.

³ Not found north of Coos Bay area, coast range only (Zobel, Roth, and Hawk 1985).

⁴ Mainly in coast range.

⁵ Evergreen hardwoods.

⁶ Sole tree dominant, or nearly so in riparian areas in serpentine region of SW Oregon, NW California (Hansen et al. 2000).

⁷ Umpqua watershed and northward.

⁸ Except in *Abies concolor* dominated areas at upper elevational limit of zone.

⁹ Both ponderosa pine (*Pinus ponderosa*) and sugar pine (*Pinus lambertiana*), which were previously more common. They still distinguish these forests, however, along with occasional *P. monticola*.

¹⁰ Reproduce here in the absence of fire, logging or other stand replacing disturbance.

REFERENCES

Barbour, M.G., and J. Major. 1977. *Terrestrial vegetation of California*. New York: John Wiley and Sons.

Franklin, J.F. and C.T. Dyrness. 1973. *Natural vegetation of Oregon and Washington*. USDA Forest Service General Technical Report PNW-8.

Hansen, E.M., D.J. Goheen, E.S. Jules, and B. Ullian. 2000. Managing Port-Orford-cedar the introduced pathogen *Phytophthora lateralis*. *Plant Disease* 84: 4-14.

Zobel, D.B.; L.F. Roth, and G.M. Hawk. 1985. *Ecology, pathology, and management of Port-Orford-cedar* (*Chamaecyparis lawsoniana*). USDA Forest Service General Technical Report PNW-184.

APPENDIX B

DISTURBANCE REGIMES IN RIPARIAN AREAS OF THE PACIFIC NORTHWEST

Table B1 Summary of Stream Characteristics and Regimes of Large Disturbance Processes (Fluvial/Geophysical and Fire) in Riparian Areas within Franklin and Dymess Vegetation Zones and Other Areas Identified and Described in Table A1

Regional Vegetation Zone	Annual precipitation	Stream Characteristics	Fluvial/Geophysical and Other Disturbances	Historic Fire Regime* and Upland Disturbances
1. West of Cascade Crest, Excluding SW Oregon and NW California				
Sitka Spruce (<i>Picea sitchensis</i>) zone	200-300 cm. Mostly or entirely as rainfall.	Ranging from small streams in steep drainages to fairly large low gradient rivers.	Flooding/sediment deposition dominant process along rivers. Infrequent debris flows in small streams ¹ .	Stand-replacing fires at a frequency ranging from 100-500+ years. Riparian areas often missed (Quaye 1982). No fire in some areas of Vancouver Island and Alaska Panhandle. Wind the dominant disturbance factor (Agee 1993).
Western Hemlock (<i>Tsuga heterophylla</i>) zone, coast ranges .	150-300 cm. Predominantly rainfall.	Ranging from small streams in steep drainages to low gradient rivers. Many headwater/higher-order streams.	Flooding/sediment deposition dominant process along rivers. Infrequent debris flows ¹ important in lower order streams.	Stand-replacing fires at a frequency ranging from 100-500+ years. No fire in some areas of Vancouver Island and Alaska Panhandle.
Western Hemlock (<i>Tsuga heterophylla</i>) zone, Cascades .	150-300 cm. Mostly rainfall, some substantive snowfall most years.	Ranging from small streams in steep drainages to moderate and high gradient rivers. Many headwater/higher-order streams.	Flooding/sediment deposition dominant process along rivers, especially with rain on snow events in watershed. Infrequent debris flows ¹ in lower order streams.	Fires of patchy mixed severity generally from 90-150 years.
Subalpine (<i>Abies amabilis</i>) zone	150-300 cm. A considerable amount as snowfall.	Mainly small to medium-sized high gradient small streams.	Flooding/mass transport often exacerbated by rain on snow events ² . Infrequent debris flows ¹ .	Stand-replacing fires at a frequency ranging from 100-500+ years. Avalanches important, And maintain corridors or tracks of non-forest Vegetation.
Willamette Valley	~100 cm. on valley floor. Mostly or entirely as rainfall.	Relatively large, low gradient Rivers on valley floor with various sized moderate to low gradient tributaries.	Flooding/sediment deposition dominant processes.	Fire frequency highly variable depending on Native American burning practices. Predominantly low severity surface fire.
2. SW Oregon and NW California				
Redwood (<i>Sequoia sempervirens</i>)	150-300 cm. Mostly or entirely as rainfall.	Ranging from small streams in steep drainages to fairly large low gradient rivers.	Flooding/sediment deposition dominant process along rivers. Overbank deposition kills trees other than redwoods, generating pure stands on terraces	Variable past fire frequency (20-500Years) depending on proximity to coast and human ignitions. Severity usually low to moderate. Post-fire runoff produces overbank sediment deposition events

(Continued on next page. See notes at end of table.)

Table B1 Continued

Regional Vegetation Zone	Annual precipitation	Stream Characteristics	Fluvial/Geophysical and Other Disturbances	Historic Fire Regime* and Upland Disturbances
2. SW Oregon and NW California (cont'd)				
Mixed evergreen <i>Pseudotsuga/sclerophyll</i> zone	60-170+ cm. Predominantly as rainfall.	Ranging from small, ephemeral streams in steep drainages to moderate and relatively high gradient rivers. Many headwater/higher-order streams	Flooding/sediment deposition dominant process along rivers and lower reaches of streams, especially following rain on snow events ² . Infrequent debris flows ¹ important in higher order streams.	Highly variable fire frequency, 3-90+ year Ranges reported, 90 year median in one study. Mixed fire severity with mostly low and moderate.
Mixed Conifer (<i>Pseudotsuga menziesii</i>) zone. (Upper elevation limit can be distinguished as the <i>Abies concolor</i> zone).	90-130 cm. Much or most as snowfall.	Ranging from small streams in steep drainages to upper reaches of relatively high gradient rivers. Many headwater/higher-order streams.	Flooding/mass transport often exacerbated by rain on snow events. Infrequent debris flows ¹ in small streams.	Fires of mixed severity at highly variable frequencies (3-150+ years). Frequency of stand replacing fire at a given location 150-350 years. Decreasing frequency with elevation.
3. Eastern Cascades				
Grand/white fir (<i>Abies grandis/concolor</i>) zone	60-120 cm. Much as snowfall.	Ranging from small streams in steep drainages to upper reaches of relatively high gradient rivers. Many headwater and lower-order streams.	Flooding/mass transport often exacerbated by rain on snow events. Infrequent debris flows ¹ in small streams.	Few data. 9-100 ^{3,4} years based on two studies. Both surface and stand-replacing fire, the latter at intervals from 140-340 years.
Western hemlock (<i>Tsuga heterophylla</i>) zone	56-170 cm. Much or most as snowfall.	Ranging from small streams in steep drainages to upper reaches of relatively high gradient rivers. Many headwater and lower-order streams	Flooding/mass transport often exacerbated by rain on snow events. Infrequent debris flows ¹ in small streams.	Fires of patchy mixed severity generally from 90-150 years likely based on relatively dry west Cascade locations.

(Continued on next page. See notes at end of table.)

Table B1 Continued

Regional Vegetation Zone	Annual precipitation	Stream Characteristics	Fluvial/Geophysical and Other Disturbances	Historic Fire Regime* and Upland Disturbances
3. Eastern Cascades (cont'd)				
Eastside Pine (<i>Pinus ponderosa</i>)	35-80 cm. Much or most as snowfall.	Ranging from small streams in steep drainages to moderate and relatively high gradient rivers. Many headwater and lower-order streams.	Flooding/mass transport often exacerbated by rain on snow events. Infrequent debris flows ¹ in small streams.	Few data. 3-33 ^{3,4} years based on two studies. Much burning by Native Americans. Predominantly low severity surface fires. Patches of even aged cohorts from stand-replacing fires may occur (Daubenmire and Daubenmire 1968).

*Figures reported are for uplands; see Section 2.2 for explanation of differences in riparian areas, which have received little direct study. See Agee (1993), Frost and Sweeney (2000), and references therein for documentation. Fire frequencies are for recent centuries. Over longer time scales frequency varied, and there was no stationary fire frequency (Whitlock, Shafer, and Marlon 2003).

¹ Though infrequent (~1-2 times/millennium) extreme events, these have profound effects (see text).

² Important in generating exceptional streamflows, causing scouring and redistribution of organic and inorganic material and creating bare surfaces.

³ Expected to be considerably longer at landscape scales that such studies that are based on locations of recorded trees, compositing samples, and that ignore the fire-free interval from tree establishment to the first fire scar (Baker and Ehle 2001).

⁴ Fires less frequent since end of Native American ignitions, arrival of cattle, and with modern fire suppression.

REFERENCES

Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests*. Washington, D.C.: Island Press.

Baker, W.L., and D. Ehle. 2001. Uncertainty in surface-fire history: The case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research* 31: 1205-1226.

Daubenmire, R.F., and J.B. Daubenmire. 1968. *Forest vegetation of eastern Washington and northern Idaho*. Washington Agricultural Experiment Station Bulletin 60.

Frost, E.J., and R. Sweeney. 2000. *Fire regimes, fire history, and forest conditions in the Klamath-Siskiyou Region: An overview and synthesis of knowledge*. Prepared for the World Wildlife Fund, Klamath-Siskiyou Ecoregion Program. <http://www.worldwildlife.org/wildplaces/kla/pubs2.cfm> (accessed September 29, 2005).

Quaye, E. 1982. The structure and dynamics of old-growth Sitka spruce (*Picea sitchensis*) forest of the Oregon Coast Range. Ph.D. diss., Oregon State University, Corvallis, OR.

Whitlock, C., S.L. Shafer, and J. Marlon. 2003. The role of vegetation change in shaping past and future fire regimes in the northwest U.S. and the implications for ecosystem management. *Forest Ecology and Management* 178: 5-21.