Riparian Management and Amphibians: Does Buffer Width Matter?

by

Virgil Clayton Hawkes
BSc, University of Victoria, 1996

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ABSTRACT

Riparian management in the Pacific Northwest has become an increasingly common way to conserve biodiversity on landscapes managed for timber production. The efficacy of two different riparian buffer widths in providing habitat for terrestrial amphibians was assessed using a Before-After-Control-Impact approach. My findings suggest that there is no global response by terrestrial amphibians to logging or to the retention of riparian management zones in the US Pacific Northwest. Rather, species showed individual responses that varied over time and between treatments and transects. Overall, a minimum riparian buffer width of 30 m was sufficient to maintain the relative abundance and richness of terrestrial amphibians at levels commensurate with pre-harvest conditions. A co-inertia analysis revealed that habitat associations changed little over time and that there were no significant differences between buffered sites suggesting that the treatments applied were biologically insignificant. The benefits of retaining riparian forest are identified and discussed in the context of maintaining biodiversity and conserving terrestrial amphibians in western Washington.

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Chapter 1 Introduction

Over the past 15 – 20 years, there have been numerous reports of amphibian declines and extirpations from many regions of the world (Banks et al. 2006; Cushman, 2006; Collins and Storfer 2003). Some of the most commonly reported causes for these declines are increased UV-B irradiation, disease, predation, and acid rain (Kolozvary and Swihart, 1999; Houlahan et al. 2000). However, the leading cause of decline, as is true for most organisms, is habitat loss and/or fragmentation (Kolozvary and Swihart, 1999; Karraker and Welsh 2006; Cushman 2006). In the US Pacific Northwest, the primary cause of habitat change and/or fragmentation is logging and associated activities such as road building.

Riparian habitat has declined in total area because of human-related activities. For example, riparian habitat was estimated to have covered 30-40 million hectares before extensive human settlement in the US. Now riparian habitat covers only 10-14 million hectares, a reduction of approximately 66% (Swift 1984). This loss is important because riparian habitats around stream edges are often the most structurally diverse areas within a landscape, have high wildlife abundance and diversity, and may be important in maintaining ecosystem integrity (Hannon et al. 2002; Naiman et al. 1993).

In recent years, forest management strategies have included the retention of forested buffer strips adjacent to the edges of streams to protect water quality and fish stocks (Castelle et al. 1994), with buffer width dependent on stream type and the presence or absence of salmonids, or other sensitive fish species. Depending on the harvest rotation, forested habitats adjacent to riparian buffer strips may never attain the features of an old-growth stand; therefore, the riparian buffer may represent the only remaining old-growth forest in certain areas. However, because riparian buffers are typically linear (i.e., aligned parallel to the stream edge), they will be influenced by the natural edge effect of the stream, and the edge effect resulting from the removal of adjacent upland forest (Yahner, 1988; Mills 1995).

The ecology of forested edges is characterized by changes in biotic and abiotic elements, both of which have been associated with negative edge effects documented in bird and plant communities, and for some species of terrestrial amphibians (deMaynadier and Hunter 1988). Although edge effects caused by timber harvest are often temporary, the cumulative effects of creating edges on a managed landscape are likely to be maximized when target stands are harvested part-way through the rotation age of the adjacent maturing stands (Harris 1984), a practice that is common in the Pacific Northwest.

Studies of the effects of timber harvest on amphibians have focused primarily on changes in abundance relative to clearcutting and not on how management strategies serve to ameliorate those effects (Dupuis et al. 1995; Grialou et al. 2000; Dupuis and Waterhouse 2001; Greenberg 2001; Welsh and Lind 2001; Aubry 2000; Biek et al. 2002; Russell et al., 2002; MacCraken 2004; Karraker and Welsh 2006). The results of these studies are equivocal, particularly with respect to species-specific responses, and most studies of the influences of habitat loss, fragmentation, or related mortality risks have not tested the population-level implications of these impacts (Carr et al. 2002; Cushman 2006). Although generalizations about the effects of timber harvest on amphibians can be made from these studies, there are currently no data on the longer-term post-treatment effects of timber harvest and its associated habitat-management strategies on amphibian populations of the US Pacific Northwest (Cushman 2006).

Of particular interest is the notion that riparian management zones (RMZs) provide habitat refuges for wildlife. The establishment of RMZs adjacent to streams in managed forests of the Pacific Northwest has been used as a landscape management tool to protect the physical and chemical attributes of perennial streams, particularly for fisheries values.

These buffer strips were originally conceived to ameliorate the effects of timber harvest on salmonids by preventing increases in water temperature and by intercepting fine sediments resulting from soil erosion (Vesely and McComb 2002). Riparian management zones often contain the only remnants of older forests on landscapes managed for timber. These zones are critical for the preservation of species diversity and abundance, and have been identified as important for habitat connectivity between upland and riparian habitats (Machtans et al. 1996; Gibbs 1998). Superficially, the preservation of riparian forest appears to provide the functions listed above; however, although several studies have examined the relationship between riparian buffer widths and abundance of amphibians (Biek et al., 2002; Vesely and McComb 2002; Crawford and Semlitsch 2007), the efficacy of riparian management zones in providing habitat for amphibians over a longer time period has not been sufficiently addressed (deMaynadier and Hunter 1995; Cushman 2006).

deMaynadier and Hunter (1995) identified the dearth of pre- and post-treatment data as one of the major problems associated with studies on the effects of habitat alteration on amphibians, although they were careful to point out why it can be difficult to obtain pre- and post-treatment data. Many studies of the relationships between populations of amphibians and logging continue to lack pre-treatment data, making it impossible to determine if the reported changes in abundance are treatment effects, site effects, or population fluctuations unrelated to site or treatment that coincided with the period of study (deMaynadier and Huner 1995; Cushman 2006; Karraker and Welsh 2006). Although attempts have been made to control for these factors (deMaynadier and Hunter 1995), neither the relative influences of individual factors nor the interactions between factors have been adequately addressed.

In addition to lack of pre-treatment data, many previous studies were limited in duration and none of them evaluated the longer-term, post-treatment interval effects of the retention of RMZs in providing habitat for wildlife. The only temporal studies of amphibian diversity and abundance in the Pacific Northwest that I could identify that were based on a Before-After-Control-Impact (BACI) study design were an earlier, largely unpublished version of my study (O'Connell et al. 2000) and a short-term study by Grialou et al. (2000). Hannon et al. (2002) reported the temporal results of a similar study on RMZs around lakes in Alberta and more recently, Perkins and Hunter (2006) reported on the temporal changes of amphibians relative to logging adjacent to headwater streams in Maine. However, the temporal component of these studies was insufficient to determine the longer, post-treatment effects of riparian management strategies on amphibians. All other studies reviewed used sites and treatments as proxies for pre-treatment conditions but they did not repeatedly measure diversity or abundance at the same sites over time, making it difficult to make inferences about the effects of logging on the abundance and diversity of amphibians (e.g., Vesely and McComb 2002).

Western Washington RMZs have been required in some form since 1976. Between 1976 and 1988, the Washington Forest Practices Rules and Regulations required "streamside management zones" (SMZ), which were intended to provide "stream bank integrity and temperature control" (Washington Forest Practices Board, 1976 and 1982). Streamside management zone regulations prescribed riparian buffers 7.5 – 15 m wide with all nonmerchantable vegetation and "sufficient merchantable timber, if any, necessary to retain 50 - 75 percent of the summer mid-day shade of the water surface" left within the SMZ (Washington Forest Practices Board 1976). In 1988 the RMZ regulations were strengthened considerably, requiring riparian buffers up to 30 m wide (Washington Forest Practices Board, 1988). The change in regulations was a result of the Timber, Fish, and Wildlife (TFW) Agreement reached in 1987 among representatives of the Washington state tribes, forest-products industry, environmental community and natural-resource agencies. The agreement sought to resolve conflicts between these diverse groups by recognizing the common goal of preservation of natural resources and at the same time the need for a viable timber industry.

In 1990, the Wildlife Steering Committee of the Cooperative Monitoring Evaluation and Research Committee (CMER) of the Timber Fish and Wildlife Agreement initiated a study to evaluate the efficacy of riparian management zones in providing habitat for wildlife. The study was designed to evaluate the abundance and diversity of wildlife in riparian zones by comparing two different buffer configurations to maturing second-growth (unlogged) reference sites. The buffer configurations were based on the RMZ guidelines mandated at the time (1988 regulations) and on modifications to the 1988 guidelines. The wildlife groups selected for study were terrestrial and aquatic amphibians, songbirds, small mammals (rodents and insectivores), and bats. A precursor to my study (O'Connell et al. 2000) compared the diversity and abundance of these wildlife groups (and others) before and immediately after logging to identify the short-term temporal effects of logging both within and between treatments. In 2001, CMER initiated a follow-up study to evaluate the longer-term effects of RMZs on wildlife. This study is the only one in Washington to evaluate the longer-term, post-treatment effects of riparian management strategies on wildlife based on data collected at the same sites.

Objectives

My research evaluated the longer-term post-treatment effects of upland forest harvest and RMZ retention on the abundance and diversity of amphibians in managed forests of western Washington. The pre-treatment and two-year post-treatment data were provided by the Washington Department of Natural Resources; I collected the ten-year post-treatment data in association with LGL Limited environmental research associates.

The over-arching goal of my research was to evaluate the effects of two different riparian management strategies on populations of terrestrial amphibians in western Washington, two years and ten years after treatment. I tested whether or not there were measurable differences in the relative abundance and diversity of amphibians relative to RMZs of two different widths. Related to my overall goal were five objectives:

1. To determine if the riparian habitat buffers retained along 3rd and 4th order streams provided habitat attributes necessary to retain diversity and abundance of amphibians;
2. To determine if there were differences in the abundance and/or diversity of amphibians in riparian buffers of two different widths;
3. To determine if either buffer width maintained the relative abundance and diversity of amphibians at levels consistent with the unlogged reference sites;
4. To determine if the relative abundance and diversity of amphibians changed in adjacent upland habitats as a result of timber harvest; and
5. To identify how habitat structure and complexity varied over time relative to treatment type to determine if habitat structure could explain differences in relative abundance or species diversity.

Study Design

My study was a component of a larger study evaluating the efficacy of riparian management zones in providing habitat for selected groups of wildlife. The larger study was initiated in 1991 with pre-treatment sampling in 1992 and 1993 (i.e., the pre-harvest sample period). The first post-treatment sampling occurred in 1995 and 1996 (i.e., the two-year post-harvest sample period), with a second post-treatment sample (my study) in 2003 and 2004 (i.e., the ten-year post-harvest sampled period). The temporal nature of this study required that sampling techniques used in the pre-harvest and two-year post-harvest sampling intervals be repeated in the ten-year post-harvest sampling interval to ensure consistency among the data sets from each sampling interval.

The study was based on a split-plot repeated-measures design with 18 sites assigned to one of three treatments. Each site was split into two distinct habitat types: riparian and upland. Riparian habitats occurred within 5 m of the ordinary high water mark adjacent to a perennial stream and extended to the point where the vegetation shifted visibly to an upland type. Upland habitats were those habitats that extended upland from the zone of transition from riparian to upland vegetation. Upland sampling occurred 100 m upslope from riparian transects.

The 18 sites were assigned to one of three treatments:

1. **Reference**: This treatment consisted of continuous stands of maturing second growth (65-75 years old) dominated by coniferous trees with no upland harvesting for the duration of the study.
2. **State**: This treatment consisted of a logged upland forest with a narrow forested buffer retained in the riparian zone. The RMZ was based on the Washington Forest Practices Rules and Regulations in place in 1988 for Type 3 (fish bearing, perennial) and Type 4 (non-fish bearing, perennial) streams for buffer width and number of

leave trees (Table 1-1). The RMZ extended from the ordinary high water mark to the line where vegetation changes from riparian to upland, but was not less than 7.5 m wide. For Type 3 streams > 1.5 m wide, the RMZ was a minimum of 15 m. For Type 4 streams, the RMZ was a minimum of 7.5 m from the ordinary high water mark. The number and arrangement of leave trees (i.e., those trees left after harvesting) was modified to accommodate the logging operation and the RMZ width was expanded as necessary to include swamps, bogs, marshes, or ponds adjacent to the stream. Limited entry into the state RMZ was allowed under the 1988 regulations.

3. **Modified**: This treatment consisted of a logged upland forest with a wider, more variable forested buffer retained in riparian zone. The RMZ was based on harvest prescriptions developed by O'Connell et al. (2000). The prescription for the modified buffer departed from the 1988 Rules and Regulations in three ways:

i) The 1988 guidelines specified a minimum canopy cover based on stream temperature classification and the elevation at the midpoint of the stream. If the cover requirement was met, selective cutting was allowed in the no-entry zone (i.e., within 7.5 m of the ordinary high water mark). The modified buffer prescription differed from the state buffer prescription in that harvest was prohibited within the no-entry zone. Cover requirements were the same as those indicated in the1988 rules [WAC-222-30-040 (2) Temperature Control, WSFPB 1988)]. Specifically, WAC-222-30-040 (2) states that:

> "All nonmerchantable vegetation that provides mid-summer and mid-day shade of the water surface should be retained; and
>
> Sufficient merchantable timber, if any, necessary to retain 50% of the summer mid-day shade of the water surface, except when ambient water temperatures exceed 15.5° C for a 7-day period. In this case, 75% of the shade should be retained."

ii) The modified prescription applied 1988 guidelines for selective harvest in state buffered RMZs to a variable width located 7.5 – 22.7 m from the ordinary high water mark. This prescription produced a buffer of at least 7.5 m from the ordinary high water mark along the riparian/upland boundary.

iii) The modified prescription increased the number of wildlife reserve trees, recruitment trees, and downed logs left for each acre harvested. State Rules and Regulations required only three wildlife reserve trees, two green recruitment trees, and two downed logs left for each harvested acre. Unless the wildlife tree violated Washington Department of Labor and Industry requirements, all wildlife reserve trees were retained on modified buffered sites. Wildlife reserve trees were defined as:

- **Type 1**: live tree with defective or deformed sound tops, trunks and roots.
- **Type 2**: dead tree with a sound top, trunk, and roots.
- **Type 3**: live or dead tree with unstable top or upper portion.
- **Type 4**: live or dead tree with unstable trunk or roots, with or without bark. This included 'soft' snags as well as live trees with unstable roots caused by root rot or fire.

A no-entry zone was specified around portions of the modified RMZ to increase the amount of undisturbed ground adjacent to the stream.

Table 1-1. Leave tree requirements per water type and average riparian management zone (RMZ) width for western Washington (WAC 222-30-020 (4c)) using January 1988 or November 1988 rules.

Water Type / avg. Width (m)	RMZ Maximum Width (m)	Ratio of Conifers: Deciduous / Size of leave trees	# Trees / 300 m (Each side) by bed material	
			Gravel / Cobble	Boulder / Bedrock
1 & 2 / ≥ 22	30	Representative of stand	50	25
1 & 2 / ≤ 22	22	Representative of stand	100	50
3 / ≥ 1.5	15	2:1 / 30 cm or next largest available	75	25
3 / ≤ 1.5	7.5	1:1 / 15 cm diameter or next largest available	25	25

Study Area

My 18 study sites were distributed throughout western Washington State, west of the Cascade Mountain Range and in the Olympic Peninsula and Southwestern Washington, Puget Trough, Western Slopes and Crest, or Washington Cascades Physiographic Provinces and in Cowlitz, Grays Harbor, King, Lewis, Pierce, and Thurston Counties (Figure 1-1).

Study sites were established in 1992 and 1993 and were selected to minimize variation in forest age and composition, elevation, moisture condition, and water type. Initially, 18 sites were selected for this study based on the following criteria:

1. Low elevation (< 620 m);
2. Second-growth forest (55-66 yr old) dominated by Douglas-fir (*Psuedotsuga menzeisii*);
3. Type 3 water by forest regulations. Type 4 was selected if streams differed only in the presence of salmonids. Water types are defined in Table 1-2;
4. Predominantly coniferous riparian canopy with deciduous tree component;
5. Stream length of a minimum of 500 m; and
6. Road access within 500 m.

Information on each site can be found in Appendix A.

Terrestrial Amphibian Sampling

Paired transects (Ruggiero et al. 1991) were established in riparian and upland habitats of each site (Figure 1-2). On one side of the stream, pitfall traps (Corn and Bury 1991, Kelsey 2000) were placed in the ground at 15 m intervals with 18 traps in the riparian and 18 traps in the adjacent upland approximately 100 m away. Riparian traps were established approximately 5 m from the ordinary high water mark. Traps were placed in the ground such that the top of the trap was level with the ground and the area around each trap (within approximately 30 cm) was cleared of sticks and other debris that could fall into the trap (Figure 1-3). Drift fences were not used in conjunction with the pitfall traps to maintain consistency with sampling methods used during the pre-harvest and two-year post-harvest sampling intervals. Each trap location was marked using a blue flag stake in the ground and blue flagging tape tied to a tree above the trap, and georeferenced using a Garmin GPS12 handheld receiver. In certain cases old pitfall trap locations could not be found, so new sites and traps were required. New pitfall traps consisted of a single can measuring 35 cm deep with a diameter of 15 cm. To reduce the number of amphibians escaping from traps, plastic inserts were placed in the opening of the cans (Figure 1-3). When previous upland transects were not found, their position on the landscape was approximated and a new transect was established. In many cases traces of the previous transect were uncovered when establishing the new transect.

Figure 1-1. Distribution of study sites and weather stations in western Washington, USA.

Table 1-2. Water typing criteria (WAC 222-16-030) used in Washington State in 1988 (Washington State Forest Practices Board (1988)).

Parameter	Water Type				
	1	2	3	4	5
Channel Width	N/A	≥ 6 m between the ordinary high water mark (OHWM)	**Anadromous Fish:** > 1.5m between OHWM **Resident Game Fish:** > 3 m between OHWM	> 0.6 m between OHWM	> 0.6 m between OHWM
Gradient	N/A	< 4%	**Anadromous Fish:** < 12% not upstream of a falls > 3m in height **Resident Game Fish:** < 12%	N/A	N/A
Flow	N/A	N/A	**Anadromous:** N/A **Resident Game:** > 0.3 CFS at summer low flow	N/A	N/A
Impoundment	N/A	Water surface area of < 0.4 ha at seasonal low flow	**Anadromous:** Water surface area of < 0.4 ha at seasonal low flow **Resident Game:** Water surface area of < 0.2 ha at seasonal low flow	N/A	N/A
Fisheries	N/A	Used by substantial numbers of anadromous or resident game fish for spawning and rearing and migration	Used by significant numbers of anadromous or resident game fish for spawning and rearing and migration	Not used by significant numbers of fish	Not used by significant numbers of fish
Diversion	N/A	Domestic use for > 100 residences or campsites. Includes upstream reach of 450 m or until the drainage area is < 50%, whichever is less	Domestic use for > 10 residences or campsites. Includes upstream reach of 450 m or until the drainage area is < 50%, whichever is less	N/A	N/A
Other	All water within their OHWM inventoried as "Shoreline of the State" excluding related wetlands	Streams flowing through campgrounds available to public having ≥ 30 campsites	Contributes > 20% of flow to Type 1 or 2 water. Anadromous fish impoundments have outlet to stream with anadromous fish	N/A	All natural waters not classified as Type 1, 2, 3 ,or 4 or seepage areas, ponds and drainways having short run-off periods

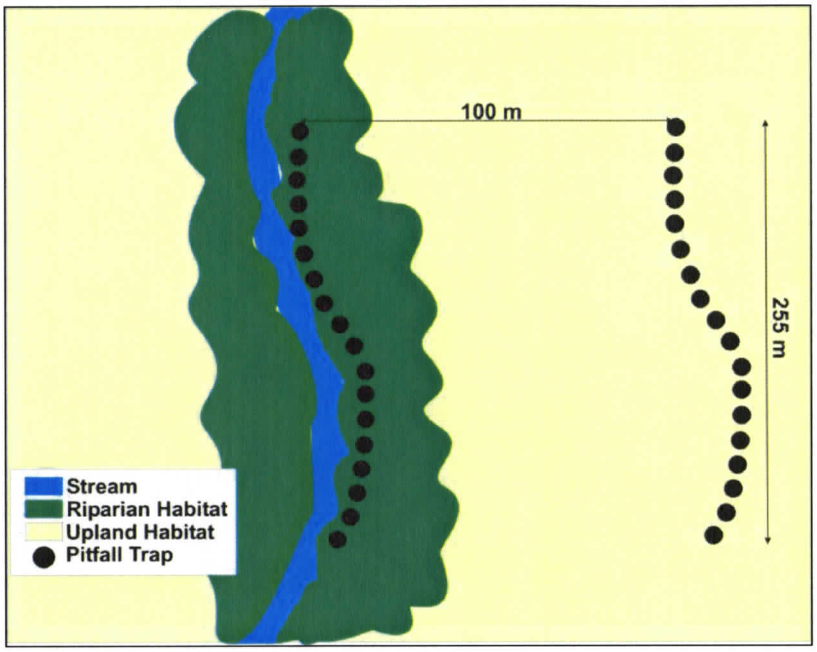


Figure 1-2. Schematic of a typical site setup to sample terrestrial amphibians using pitfall traps.

Not all sites were sampled in each year (Table 1-3). For example, 13 of 18 sites were sampled in 1992 while all 18 sites were sampled in 1993, 1995, and 1996. Some time after 1996 one of the reference sites was logged, which necessitated the addition of a new reference site in 2003. The new site fit the criteria used in 1992. Also, in 2003, one of the modified buffered sites (Griffen Creek) received a silvicultural treatment (brushing and thinning in the upland) that was not applied to all modified buffered sites. As a result, this site no longer varied through time equally with the other sites and was excluded from the study.

Table 1-3. Western Washington terrestrial amphibian sampling period for each sampling interval (SI).

SI[a]	Year	Start	End	Days	Sites
1	1992	30-Oct-92	14-Dec-92	45	13
	1993	6-Oct-93	3-Nov-93	28	18
2	1995	14-Oct-95	16-Nov-95	33	18
	1996	13-Oct-96	14-Nov-96	32	18
3	2003	16-Oct-03	1-Dec-03	46	17*
	2004	4-Oct-04	16-Nov-04	43	17*

[a] SI = Sample Interval *The Griffen Creek modified site was not sampled because of modifications to the upland transects that did not occur at all sites

Figure 1-3. Photograph of a typical pitfall trap. The yellow object is the plastic insert used to prevent escapes.

Traps remained open for 28 consecutive nights (per site) and were checked every 2-5 days. Approximately 5 cm of water was put into each trap to prevent amphibian desiccation. I also placed a small sponge, a small moss mat, or a small piece of woody debris in each trap so that captured amphibians could stay out of the water and not drown.

O'Connell et al. (2000) checked pitfall traps approximately weekly, with all animals removed from the pitfall traps and the field. Any live-captured amphibians were removed to a laboratory refrigerator and retained until the completion of the trapping period, after which they were returned to their original site of capture. For this study, I elected to toe-clip amphibians and release them near the pitfall trap. I also increased the frequency of trap-checking to facilitate the capture of live amphibians.

Amphibians were weighed to the nearest 0.25 gram using a Pesola® Scale. I recorded snout-vent length (SVL) and total length (TL) to the nearest millimeter for salamanders and snout-urostyle length (SUL) for frogs. Where possible, I assigned each animal to a sex and age class.

I toe-clipped amphibians of sufficient size (juvenile salamanders ≤ 35 mm SVL were not marked) using surgical iris scissors and I removed no more than three toes per individual. Each animal was given a unique clip to ensure that animals were not double-counted. In addition to toe-clipping, I photographed the dorsal side of most amphibians captured, which, for certain species can function as a secondary mark (especially true for *Plethodon vehiculum* [Davis and Ovaska 2001] and *Rana aurora* [Hawkes, unpublished data]).

Because it was not possible to identify the direction of travel a particular amphibian had taken prior to falling into a pitfall trap, I released each amphibian approximately 2 m downstream of the trap in which it was captured, typically under or near a suitable cover object. Dead amphibians were measured and assigned to an age-class (e.g., adult, juvenile) and preserved in formalin if they had not been partially consumed by small mammals or were not too decomposed.

Chapter 2
The Influence of Riparian Buffer Width on Amphibian Relative Abundance and Species Richness

Introduction

Riparian areas in forested landscapes have been recognized for high species richness of amphibians (McComb et al. 1993, Dupuis et al. 1995, Perkins 2004), yet little is known about the persistence of amphibians in mature forest fragments such as unharvested riparian buffers surrounded by clearcuts (Perkins and Hunter 2006). In certain regions of Canada and the United States, amphibians have been shown to be sensitive to forest management (deMaynadier and Hunter 1998, DeGraaf and Yamasaki 2002; Perkins and Hunter 2006) and the short-term adverse effects of timber-harvesting on terrestrial amphibians have been well documented in the literature (Blymer and McGinnes 1977, Pough et al. 1987, Bury 1983, Ash 1988, Petranka et al. 1993, Ash and Bruce 1994, Petranka et al. 1994, deMaynadier and Hunter 1995, Dupuis et al. 1995, Means et al. 1996, Mitchell et al. 1996, Ash 1997, Messere and Ducey 1998, Sattler and Reichenbach 1998, Herbeck and Larsen 1999, Harpole and Haas 1999, Bartman et al. 2001, Duguay and Wood 2002, Knapp et al. 2003).

Manipulative forest management experiments with pre- and post-treatment data, random assignment of replicates to treatments, and analyses over a large spatial scale are rare in the literature due to the difficulty of coordinating harvest scheduling and specifications among multiple landowners, and obtaining adequate funding (deMaynadier and Hunter 1995). Furthermore, even studies with pre- and post-treatment data can be weakened due to ecological time lags; the longevity of some species may mean that it could take several years to observe a treatment effect (Perkins and Hunter 2006). The low motility of amphibians relative to other forest vertebrates makes them useful for determining the effect of harvesting practices on a local scale because different treatments are unlikely to be confounded by temporal variation or immigration into suboptimal habitat (Sinsch 1990, deMaynadier and Hunter 1995). Amphibians are also likely to play an important role in ecosystem dynamics by structuring communities of forest decomposers (Burton and Likens 1975, Hairston 1986, Wyman 1998) and because they are often the most abundant vertebrates in temperate forest ecosystems (Burton and Likens 1975, Hairston 1986, Petranka and Murray 2001, DeGraaf and Yamasaki 2002).

Declines in the relative abundance of amphibians have been reported from sites harvested using silvicultural techniques such as clearcut, shelterwood, group selection, and leavetree (Harpole and Haas 1999). Herbeck and Larsen (1999) reported that terrestrial plethodontid salamanders were reduced to very low numbers after intensive harvest on mature forest (>70 years old), probably due to decreased microhabitat availability. Similarly, Duguay and Wood (2002) discovered lower relative abundance of salamanders in 15 year-old forests regenerating after timber harvest compared to mature second-growth forests (>60 years old), and Grialou et al. (2000) suggested that plethodontid salamander abundance declined immediately after logging in Washington State.

The evidence that timber harvest negatively affects some amphibian populations seems compelling. However, most studies have focused primarily on changes in abundance relative to logging (e.g., clearcutting, shelterwood, etc.) and not on how management strategies might serve to ameliorate those effects. Results from studies specific to the Pacific Northwest (including portions of British Columbia) are equivocal, particularly when it comes to species-specific responses, and most studies of the influences of habitat loss, fragmentation, or related mortality risks have not assessed the population-level implications of those impacts (Dupuis et al. 1995; Dupuis and Waterhouse 2001; Greenberg, 2001; Welsh and Lind, 2001; Aubry, 2000; Biek et al. 2002; Carr et al. 2002; Russell et al., 2002;

MacCraken 2004; Cushman 2006; Karraker and Welsh, 2006). Although some generalizations about the effects of timber harvest on the relative abundance of amphibians can be made from those studies, no data exist on the longer-term, post-treatment effects of timber harvest and associated habitat-management strategies on the relative abundance or species richness of amphibians in the US Pacific Northwest (Cushman 2006). Specifically, there has not been a single longer-term (≥ 10 year) study (based on a before-after-control-impact [BACI] design) on the utility of riparian management zones for maintaining the relative abundance and richness of terrestrial amphibians after logging.

Objectives

My objectives were to compare the relative abundance and species richness of terrestrial amphibians among and within three sampling intervals (pre-treatment, two-year post-treatment, and ten-year post-treatment). Specifically, I wanted to determine if there were measurable differences in relative abundance and species richness at the state buffered or modified buffered treatments compared with the unlogged reference sites to address two related but distinct questions: 1) does riparian buffer width matter? and 2) does logging matter? The magnitude and direction of the difference indicated riparian management zone effectiveness. Moreover, a measurable difference in relative abundance and/or richness values between the treatments and reference sites provided an indication of the minimum buffer width required to maintain relative abundance and richness values at levels consistent with the reference sites and/or pre-harvest levels.

Methods

General study design, site distribution, and field sampling methods are described in Chapter 1. Using the pitfall catch data, I compared the relative abundance of seven abundant species of amphibians (Western Red-backed Salamander, Ensatina, Red-legged

Frog, Coastal Tailed Frog, Pacific Giant Salamander, Northwestern Salamander, and Rough-skinned Newt) within and among sampling intervals for each treatment and habitat type (riparian and upland).

Because climatic conditions can affect the surface activity of amphibians, I obtained daily weather data from the Western Regional Climate Center Desert Research Institute (2215 Raggio Parkway Reno, NV 89512) for the period 1 January 1990 – 31 January 2005 for four stations in western Washington (Elma, Longview, Packwood, and Landsburg). The four stations were selected because they were centrally located among my study sites (Figure 1-1; Table 2-1). The weather data were obtained to evaluate whether or not climatic conditions could have influenced species activity, thereby affecting detectability and measures of species richness and relative abundance.

Table 2-1. Weather stations in western Washington queried for daily temperature and precipitation data for the period 1990 – 2004.

Station	Site Name	Treatment	General Area
Elma, Washington 452531	Blue Tick	Modified	Capitol State Forest
	Ms Black	Modified	
	Night Dancer	State	
	Porter Creek	Reference	
	Potpourri	State	
	West Fork Falls Creek	Reference	
Longview 454769	Abernathy	Reference	Southwest Washington
	Ryderwood 1557	State	
	Ryderwood 860	Modified	
Packwood 456262	Elbe Hills	Reference	West-central Washington
	Eleven 31	Modified	
	Eleven 32	State	
	Kapowsin	State	
	Side Rod	Modified	
	Simmons Creek	State	
	Vail	Reference	
Landsburg 454486	Griffin Creek	Modified	Cedar River Watershed
	Hotel Creek	Reference	
	Taylor Creek	Reference	

Statistical Analyses

Statistical analyses were performed using SAS V9.1 (© 2002-2003), R V2.2.1 (© 2005), and Microsoft Excel 2002 (© 1985-2003). All data were assessed for normality by an inspection of residuals. Comparisons of relative abundance (mean catch per 100 trap nights) were done using log-transformed means ($\log(x{+}1)$), which approximated a normal distribution. Where appropriate, *post hoc* multiple range tests were used that accounted for experiment-wise error and thereby reduced Type I Errors (Shaffer 1995). When pairwise comparisons of means were made, the Tukey HSD method (Miller 1981) was applied to control the family-wise error (FWE) rate. The critical value of alpha was set at 0.05 for all analyses, although values between 0.05 and 0.1 are also discussed.

Species Richness and Diversity

I used the number of species found in each habitat type (i.e., riparian or upland) of each site during each sampling interval as a measure of species richness. Species richness data from riparian transects were used to examine the effect of buffer width. To test whether logging influenced species richness or diversity, I combined data from both the state and modified riparian buffer treatments. Because the uplands of both treatments were clearcut, pooling the treatments provided a sense of whether or not the retention of riparian habitat, regardless of width, provided for the persistence of species richness.

I used Morisita's coefficient of similarity (*C*) as a measure of community similarity because of its superior utility, relative to other measures, in pairwise comparisons of communities (Krebs 1999). Morisita's index (Morisita 1959; Horn 1966; Brower et al. 1990) measures community similarity and is based on Simpson's index of dominance (Simpson 1949). It calculates the probability that specimens randomly drawn from two sites will be of the same species, relative to the probability that specimens randomly drawn from the same site will be of the same species. This index is desirable because sample size has little influence on its calculation (Morisita 1959; Wolda 1981). Morisita's index returns a value from 0 (no similarity) to 1 (identical).

Relative Abundance

I tested variation in relative abundance only for the most common species; sample size was too small for analysis of other species (e.g., Dunn's Salamander, Pacific Treefrog, Long-toed Salamander, Southwest Torrent Salamander, Cascade Torrent Salamander, Cascade Frog, and Western Toad). Using PROC MIXED in SAS, I ran repeated-measures ANOVAs to test hypotheses about variation in relative abundance, followed by orthogonal and non-orthogonal contrasts (Table 2-2) of the main effects (treatment, transect, sampling interval) and their interactions. The main experimental units for which measurements were repeatedly collected were the individual transects in riparian and upland habitats, and the data from each transect were pooled to derive a treatment mean for each of the three sampling intervals.

Contrasts were grouped into two sets of questions: differences *among* and differences *within* sampling intervals. In each question set, contrasts were used to answer questions about the mean relative abundance of the more common species detected. Based on the objectives of my study, the sampling intervals, treatments, and transects were grouped to best answer the questions of differences between the state and modified buffered treatments relative to the reference sites over time. The comparisons derived were based on the following assumptions:

1. All sites selected for this study were similar enough that results derived for one site could be extrapolated across all sites of a particular treatment and as such, pooling of sites into treatments was acceptable.

2. The upland habitats of the state and modified buffered treatments represented the same treatment and thus could be pooled into a post-cut condition defined by clearcut logging followed by replanting.
3. A comparison of the reference site uplands with the pooled state and modified buffered uplands (i.e., pre-cut vs. post-cut) addresses logging effects (i.e., does logging uplands affect the relative abundance of terrestrial amphibians?)
4. A comparison of the reference riparian transects to the pooled state and modified buffered condition determines whether logging affects relative abundance of terrestrial amphibians irrespective of buffer width.
5. A comparison between riparian transects of the modified and state buffered treatments provides a measure of the effect of a wide buffer vs. a narrow buffer and the effect that buffer width has on the relative abundance of terrestrial amphibians.

The contrasts in Table 2-2 consist of two question sets. Question set 1 consists of 24 contrasts that compare the relative abundance of terrestrial amphibians across time to determine if there are temporal relationships due to treatment or habitat type (transect). The 18 contrasts in question set 2 evaluate relative abundance within each sampling interval relative to treatment and habitat type. This is particularly important for the pre-treatment sampling interval to establish a baseline of similarity or difference prior to treatment application.

The maximum number of pairwise comparisons that could have been made for each species was 153, of which I made 42: 22 of these are orthogonal. The 20 non-orthogonal contrasts are designed to ask pertinent questions of the data to determine if there are measurable treatment effects on the relative abundance of amphibians across time. Non-orthogonal contrasts ask specific questions and are a compromise between a “fishing expedition" (all possible pairwise *a posteriori* comparisons) and completely orthogonal (and therefore independent) contrasts. Contrasts are preferred to multiple ANOVAs with post hoc multiple range tests to control FWE because they can reduce the number of questions asked of the data (and therefore avoid data mining) and because many of the other possible comparisons of the means are not of interest.

There is little clarity in the literature regarding the "right" way to approach the use of non-orthogonal contrasts. Some authors have indicated that non-orthogonal contrasts are acceptable provided the redundancy is noted (Mead 1990). Other authors have commented that orthogonality is desirable but not essential because a reasonable approximation of the probabilities exists for non-orthogonal contrasts. Miller (1981) indicated that because multiple comparisons are being made (regardless of orthogonality) the results should be corrected for experiment-wise error using a correction factor such as Scheffé, Bonferonni, or Sidak. Miller (1981) discusses methods for pair-wise comparison that can be adapted for general contrasts and suggests that Bonferonni be used for additive inequality and Sidak for multiplicative inequality and that these corrections should be applied when the number of comparisons is large. The term "large" is vague and conveys nothing about when to account for experiment-wise error when using contrasts analyses in repeated-measures ANOVAs. I did not consider the number of comparisons to be large relative to the number of comparisons that were possible for each species. In addition, because I was analyzing a temporal data set that included 3 sampling intervals with 17 contrasts per sampling interval, I could have generated up to 51 orthogonal contrasts. Based on the ambiguity in the literature, I elected not to adjust the critical value of alpha.

Table 2-2. Non-orthogonal contrasts used to identify differences in relative abundance (RA) among and within sampling intervals (SI) relative to treatment and transect. SI 1 = 1992-93; SI 2 = 1995-96; SI 3 = 2003-04.

	Sampling Interval, Transect, and Treatment type	Question
Among	REFERENCE RIPARIAN - SI 1 vs SI 2	Is RA different in SI 1 compared to SI 2 for reference riparian transects?
	REFERENCE RIPARIAN - SI 1 vs SI 3	Is RA different in SI 1 compared to SI 3 for reference riparian transects?
	REFERENCE RIPARIAN - SI 2 vs SI 3	Is RA different in SI 2 compared to SI 3 for reference riparian transects?
	REFERENCE RIPARIAN - pre-cut vs post-cut	Is RA pre-harvest different than post-harvest for reference riparian transects?
	MODIFIED RIPARIAN - SI 1 vs SI 2	Is RA different in SI 2 compared to SI 3 for modified riparian transects?
	MODIFIED RIPARIAN - SI 1 vs SI 3	Is RA different in SI 1 compared to SI 2 for modified riparian transects?
	MODIFIED RIPARIAN - SI 2 vs SI 3	Is RA different in SI 1 compared to SI 3 for modified riparian transects?
	MODIFIED RIPARIAN - pre-cut vs post-cut	Is RA pre-harvest different than post-harvest for modified riparian transects?
	STATE RIPARIAN - SI 1 vs SI 2	Is RA different in SI 1 compared to SI 2 for state riparian transects?
	STATE RIPARIAN - SI 1 vs SI 3	Is RA different in SI 1 compared to SI 3 for state riparian transects?
	STATE RIPARIAN - SI 2 vs SI 3	Is RA different in SI 2 compared to SI 3 for state riparian transects?
	STATE RIPARIAN - pre-cut vs post-cut	Is RA pre-harvest different than post-harvest for state riparian transects?
	REFERENCE UPLAND - SI 1 vs SI 2	Is RA different in SI 1 compared to SI 2 for reference upland transects?
	REFERENCE UPLAND - SI 1 vs SI 3	Is RA different in SI 1 compared to SI 3 for reference upland transects?
	REFERENCE UPLAND - SI 2 vs SI 3	Is RA different in SI 2 compared to SI 3 for reference upland transects?
	REFERENCE UPLAND - pre-cut vs post-cut	Is RA pre-harvest different than post-harvest for reference upland transects?
	MODIFIED UPLAND - SI 1 vs SI 2	Is RA different in SI 1 compared to SI 2 for modified upland transects?
	MODIFIED UPLAND - SI 1 vs SI 3	Is RA different in SI 1 compared to SI 3 for modified upland transects?
	MODIFIED UPLAND - SI 2 vs SI 3	Is RA different in SI 2 compared to SI 3 for modified upland transects?
	MODIFIED UPLAND - pre-cut vs post-cut	Is RA pre-harvest different than post-harvest for modified upland transects?
	STATE UPLAND - SI 1 vs SI 2	Is RA different in SI 1 compared to SI 2 for state upland transects?
	STATE UPLAND - SI 1 vs SI 3	Is RA different in SI 1 compared to SI 3 for state upland transects?
	STATE UPLAND - SI 2 vs SI 3	Is RA different in SI 2 compared to SI 3 for state upland transects?
	STATE UPLAND - pre-cut vs post-cut	Is RA pre-harvest different than post-harvest for state upland transects?
Within	SI 1 RIPARIAN - Reference vs cut	In SI 1 was riparian RA at the references different from the treatments?
	SI 1 RIPARIAN Reference vs. State	In SI 1 was riparian RA different between the reference and state?
	SI 1 RIPARIAN - Modified vs. State	In SI 1 was riparian RA different between the modified and state?
	SI 1 RIPARIAN Reference vs. Modified	In SI 1 was riparian RA different between the modified and reference?
	SI 2 RIPARIAN - Reference vs cut	In SI 2 was riparian RA at the references different from the treatments?
	SI 2 RIPARIAN - Reference vs State	In SI 2 was riparian RA different between the reference and state?
	SI 2 RIPARIAN - Modified vs. State	In SI 2 was riparian RA different between the modified and state?
	SI 2 RIPARIAN - Reference vs Modified	In SI 2 was riparian RA different between the reference and modified?
	SI 3 RIPARIAN - Reference vs cut	In SI 3 was riparian RA at the references different from the treatments?
	SI 3 RIPARIAN - Reference vs State	In SI 3 was riparian RA different between the reference and state?
	SI 3 RIPARIAN - Modified vs. State	In SI 3 was riparian RA different between the modified and state?
	SI 3 RIPARIAN - Reference vs Modified	In SI 3 was riparian RA different between the reference and modified?
	SI 1 UPLAND - Reference vs cut	In SI 1 was upland RA at the references different from the treatments?
	SI 1 UPLAND - Modified vs. State	In SI 1 was upland RA different between the modified and state?
	SI 2 UPLAND - Reference vs cut	In SI 2 was upland RA at the references different from the treatments?
	SI 2 UPLAND - Modified vs. State	In SI 2 was upland RA different between the modified and state?
	SI 3 UPLAND - Reference vs cut	In SI 3 was upland RA at the references different from the treatments?
	SI 3 UPLAND - Modified vs. State	In SI 3 was upland RA different between the modified and state?

Results

Field Sampling

A total of 100,140 trap nights (riparian = 50,066; upland = 50,074) were amassed for all sites and sampling intervals. The highest trap night total was obtained for the state buffered sites (n = 34,668) and the two-year post-logging sampling interval had more trap nights (n = 36,288) than both the pre-harvest and ten-year post-harvest intervals. Overall, the number of trap nights per treatment and transect did not vary markedly across time with the exception of the modified treatment in the ten-year post-treatment sampling interval (Table 2-3) because of the removal of Griffen Creek from the study. The number of site visits increased in the ten-year post-harvest sampling interval (2003 & 2004) because of the desire to reduce trap mortalities.

Sampling intensity was measured as the number of pitfall trap nights for each site and treatment (Table 2-3). Site- and trap-specific data were not available for either the pre-treatment or the two-year post-treatment sampling periods (these data were provided by the Washington State Department of Natural resources). For these intervals, I derived a correction factor that was based on the number of non-functional traps per habitat type at each site during the ten-year post-harvest sampling interval. In most cases, the adjustment to the number of pitfall trap nights was minimal or nil. The values calculated for the ten-year post-treatment sampling interval reference sites were used when calculating average trap nights for the pre-harvest and two-year post-harvest sampling intervals. The average number of trap nights obtained for each of the buffered treatments in the ten-year post-treatment interval was used to calculate relative abundance for the pre-harvest and two-year post-harvest intervals. Values in Table 2-4 were used in all subsequent analyses.

Table 2-3. Total trap nights by treatment, transect, and sampling interval.

	SI 1[a]			SI2[a]			SI3[a]			Totals		
Treatment	Rip	Upl	Tot	Rip	Upl	Tot	Rip	Upl	Tot	Rip	Upl	Tot
Control	5040	5040	10080	6048	6048	12096	5802	5825	11627	16890	16913	33803
Modified	5040	5040	10080	6048	6048	12096	4754	4739	9493	15842	15827	31669
State	5544	5544	11088	6048	6048	12096	5742	5742	11484	17334	17334	34668
	15624	15624	31248	18144	18144	36288	16298	16306	32604	50066	50074	100140

[a]SI 1 = 1992-93; SI 2 = 1995-96; SI 3= 2003-2004

Table 2-4. Pitfall trap nights calculated for each site during each sampling interval (SI). Values for SI 1 and SI 2 are based on averages of values obtained during SI 3.

		SI 1[a]				SI 2[a]				SI 3[a]			
	Pitfall Traps	1992		1993		1995		1996		2003		2004	
Treatment	Site Name	Rip	Upl	Rip	Upl	Rip	Upl	Rip	Upl	Rip	Upl	Rip	Upl
Reference	Abernathy			504	504	504	504	504	504	486	486	486	486
Reference	Elbe Hills			504	504	504	504	504	504	486	486	462	465
Reference	Hotel Creek	504	504	504	504	504	504	504	504	486	486	468	468
Reference	Porter Creek	504	504	504	504	504	504	504	504	468	468	486	486
Reference	Taylor Creek	504	504	504	504	504	504	504	504	486	482	468	468
Reference	Vail[1]	504	504	504	504	504	504	504	504				
Reference	West Fork Falls Creek[2]									558	558	462	486
Modified	Blue Tick			504	504	504	504	504	504	486	461	486	423
Modified	Eleven 31	504	504	504	504	504	504	504	504	432	432	468	468
Modified	Griffen Creek[3]	504	504	504	504	504	504	504	504				
Modified	Ms Black	504	504	504	504	504	504	504	504	524	570	486	513
Modified	Ryderwood 860	504	504	504	504	504	504	504	504	432	432	486	486
Modified	Side Rod			504	504	504	504	504	504	486	486	468	468
State	Eleven 32	504	504	504	504	504	504	504	504	432	432	468	468
State	Kapowsin	504	504	504	504	504	504	504	504	504	504	468	468
State	Night Dancer			504	504	504	504	504	504	486	486	486	486
State	Potpourri	504	504	504	504	504	504	504	504	468	468	486	486
State	Ryderwood 1557	504	504	504	504	504	504	504	504	486	486	486	486
State	Simmons Creek	504	504	504	504	504	504	504	504	504	504	468	468

[a]SI 1 = 1992-93; SI 2 = 1995-96; SI 3= 2003-2004; [1] Vail was logged after SI2; [2] West Fork Falls Creek replaced Vail; [3] Griffen Creek dropped from study in summer 2003 due to silvicultural practices that occurred there but no where else.

Environmental Conditions

Temperature and precipitation data were plotted for the months of October and November (pooled) for each year of each sampling period to determine if environmental conditions were similar (Figure 2-1; Figure 2-2). Mean temperature varied among years and stations; however, the variation was not enough to affect surface activities of amphibians and was within the range of temperature conditions considered suitable for amphibian sampling in the Pacific Northwest (Blaustein et al. 1995). The relative frequency of rain days (i.e., days with > 1 mm of rain) did not differ among years or weather stations ($x_{15}^2 = 9.91$; $p = 0.83$).

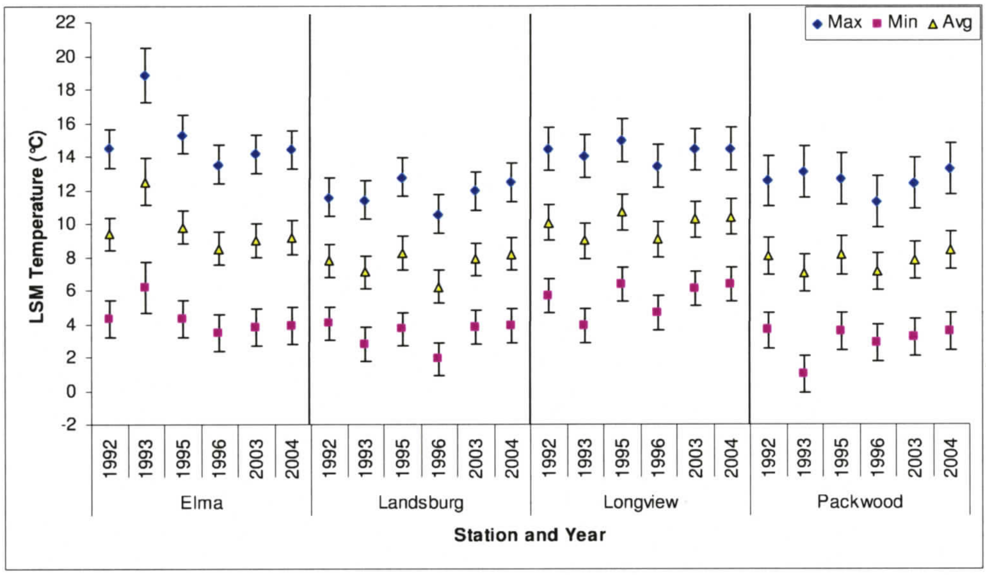


Figure 2-1. Maximum, minimum, and average temperatures (° C) (± 95% CI) for the period 1 October through 30 November for each year of amphibian sampling in western Washington. LSM = least squared mean.

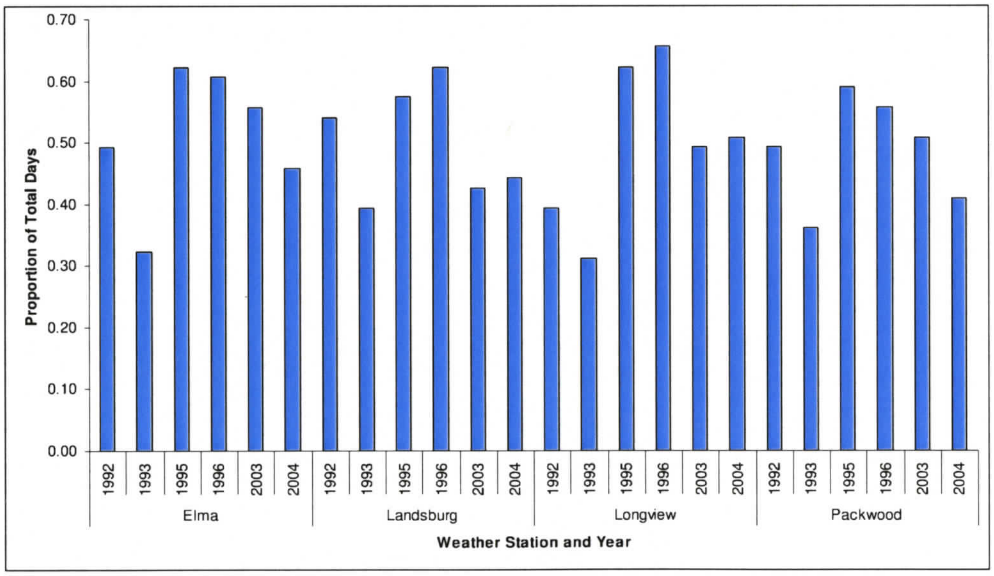


Figure 2-2. Proportion of days with (i.e., > 1 mm) rain (i.e., < 1 mm) for the period 1 October through 30 November for each year of amphibian sampling in western Washington. Only data from October were available for Elma in 1993.

Species Richness

Fourteen species of amphibians were documented from all sites across all sampling intervals (Table 2-5). Species richness did not differ relative to treatment, habitat type, or sampling interval ($F_{1,4} = 0.25$; $p = 0.64$; Figure 2-3). Certain species (e.g., Western Toad and Cascade Frog) were detected in only one sampling interval while other species (e.g., Western Red-backed Salamander and Ensatina) were detected in every sampling interval and on all transects of all sites (Table 2-5). In addition, no consistent patterns of change in species richness were observed with the exception of upland transects of the modified treatment that consistently declined over all three sampling intervals (Figure 2-3).

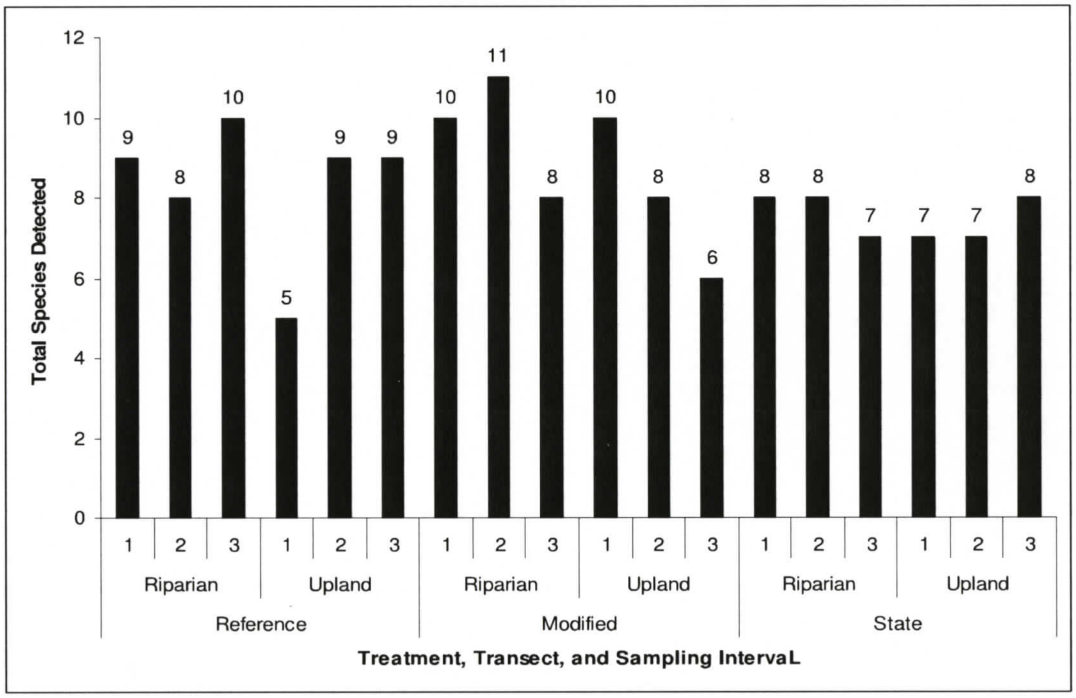


Figure 2-3. Total species detected per treatment, transect, and sampling interval. 1 = 1992 & 1993; 2 = 1995 & 1996; 3 = 2003 & 2004.

Table 2-5. Amphibian species detected per sampling interval, treatment, and transect. P = presence; blanks =not detected. R = Riparian, U = Upland, T = Treatment.

	Pre-harvest									Two-years Post-harvest									Ten-years Post-harvest								
	Reference			Modified			State			Reference			Modified			State			Reference			Modified			State		
Species	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**	**R**	**U**	**T**
Ascaphus truei Tailed Frog	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Bufo boreas Western Toad																										P	P
Hyla regilla Pacific Treefrog					P	P				P		P					P	P				P		P			
Rana aurora Red-legged Frog	P		P	P	P	P	P	P	P	P	P	P	P	P	P	P		P	P	P	P	P	P	P	P	P	P
Rana cascadae Cascade Frog										P		P															
Ambystoma gracile Northwestern Salamander	P	P	P	P	P	P	P	P	P	P	P	P	P		P	P	P	P	P	P	P	P	P	P	P	P	P
Ambystoma macrodactylum Long-toed Salamander	P		P	P	P	P							P	P	P							P	P	P			
Dicamptodon tenebrosus Pacific Giant Salamander	P	P	P	P	P	P	P	P	P	P	P	P	P		P	P	P	P	P	P	P	P		P	P		P
Ensatina eschscholtzii Ensatina	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Plethodon dunni Dunn's Salamander	P		P	P		P	P		P	P	P	P				P		P		P	P						
Plethodon vehiculum Western Red-backed Salamander	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Rhyacotriton cascadae Cascade Torrent Salamander				P		P											P	P				P		P			
Rhyacotriton keezeri Southwestern Torrent Salamander	P		P		P	P					P	P	P		P				P	P	P	P	P	P	P	P	P
Taricha granulosa Rough-skinned Newt				P	P	P	P	P	P	P	P	P		P	P		P	P	P	P	P	P	P	P	P		P
Species Richness	**9**	**5**	**9**	**10**	**10**	**12**	**8**	**7**	**8**	**10**	**9**	**11**	**8**	**6**	**9**	**7**	**8**	**10**	**8**	**9**	**9**	**11**	**8**	**11**	**8**	**7**	**9**

During the pre-treatment sampling interval (1992-93), 12 species of amphibians were captured at all sites (*n* = 18), with 11 on riparian transects and 10 on upland transects (Table 2-5). Mean number of species (±SE) did not differ significantly between riparian (4.1 ± 0.35) and upland habitats (all sites combined) (3.4 ± 0.35; $F_{1,34} = 2.2$; $p = 0.15$), nor did they differ significantly within assigned treatment types on riparian or upland transects (Figure 2-4). The mean number of species (riparian and upland data combined) detected at the modified buffered sites (4.5 ± 0.4) was higher than the reference (3.7 ± 0.4) and state buffered sites (3.1 ± 0.4), a difference that was marginally significant ($F_{2,33} = 3.02$; $p = 0.06$) (Figure 2-4). The modified buffered treatment had the highest number of species on both the riparian and upland transects Figure 2-4).

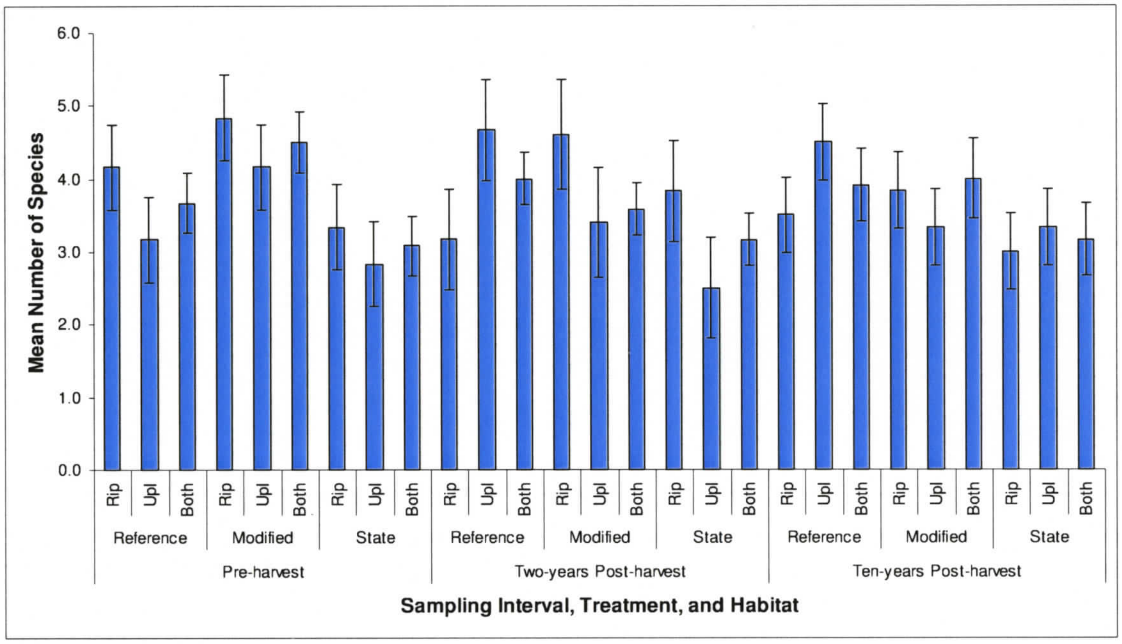


Figure 2-4. Mean number (± SE) of species by sampling interval, treatment, and habitat type. Rip = Riparian; Upl = Upland.

During the two-year post-treatment sampling interval (1995-96), 13 amphibian species were detected (riparian, *n* = 12; upland *n* = 12) (all sites combined; Table 2-5). The number of species detected on riparian transects ranged from seven at state sites to ten at the reference sites; eight species were documented from riparian transects at modified buffered sites (Figure 2-3). The number of species detected per treatment and transect did not vary among treatments ($F_{2,33}$ = 1.31; p = 0.28). Similar to the pre-harvest period, the modified buffered sites had the highest number of species (on average) on riparian transects with the highest number of species detected on upland transects occurring at the reference sites (Figure 2-4).

The ten-year post-harvest data followed a trend similar to the two-year post–harvest data with the average number of species detected per site within each sampling interval not varying significantly relative to transect ($F_{2,31}$ = 0.8, p = 0.46; Figure 2-4). On riparian transects, the highest average number of species (3.8 ± 0.51; Figure 2-4) occurred at the modified buffered treatment. In the upland, the reference group that had the highest average number of species (4.5 ± 0.51; Figure 2-4).

The most obvious trend noted across time for all treatments was that the riparian habitats of the modified buffered sites always had the highest mean number of species and for two of the three sampling intervals, the highest mean number of species on upland habitats was documented at the reference sites.

Community and Diversity Comparisons

Community similarity (Morisita's *C*) remained relatively constant on riparian habitats of the reference sites across time, with similar amphibian communities before and after logging (Figure 2-5). Similarity between riparian habitats in the two-year and ten-year post-harvest sampling intervals was also high (C = 0.82), providing an indication of community stability over time (Figure 2-5). The slight reduction in similarity noted for the two- and ten-year post-harvest amphibian communities is attributable to the non-detection of Pacific Treefrog, Dunn's Salamander, and Cascades Frog in the ten-year post-harvest sampling interval. The number of Ensatinas and Western Red-backed Salamanders was lower in the ten-year post-harvest sampling interval, which influenced the results. One species, Columbia Torrent Salamander, was not detected two years after logging, with only two captures ten years after harvest.

Amphibian communities of the modified buffered treatment were similar in all three sampling intervals. A comparison of the two post-harvest sampling intervals revealed that the communities had changed slightly on both riparian (C = 0.69) and upland habitats (C = 0.72). The changes were again attributable to differences in total captures of certain species (e.g., Western Red-backed Salamanders, Ensatinas and Red-legged Frogs) or the detection of species in one sampling interval but not the other. The amphibian communities sampled during the pre-harvest interval were similar to the two-year and ten-year post-harvest sampling periods on both riparian and upland transects and the community sampled in 1995-1996 was the same as the community sampled in 2003-2004 (Figure 2-5).

There was little change in community similarity among sampling intervals on both riparian and upland habitats. However, there were some notable changes at the treatment level within and across time (Figure 2-6). First, amphibian communities on riparian and upland transects of the state buffered treatments were the least similar and lower in diversity than both the modified buffered and reference treatments prior to logging. Second, amphibian communities on riparian and upland transects became more similar at all treatments two-years after logging. Third, the amphibian communities of the reference and modified buffered sites became more dissimilar ten-years after logging relative to the pre-harvest and two-year post-logging intervals with the largest change observed for the reference sites. Last, the ten-year post-harvest amphibian communities of the state buffered sites were equal to the two-year post-harvest period and more similar than the pre-harvest communities of the modified buffered and reference sites (Figure 2-6). Pre-logging and immediate post-logging (1995-1996) community similarity between riparian and upland habitats was highest for the modified buffered sites. Two years after logging, similarity was highest for the state buffered sites. Amphibian communities on riparian and upland habitats at the reference sites had the lowest similarity coefficient ten years after harvest.

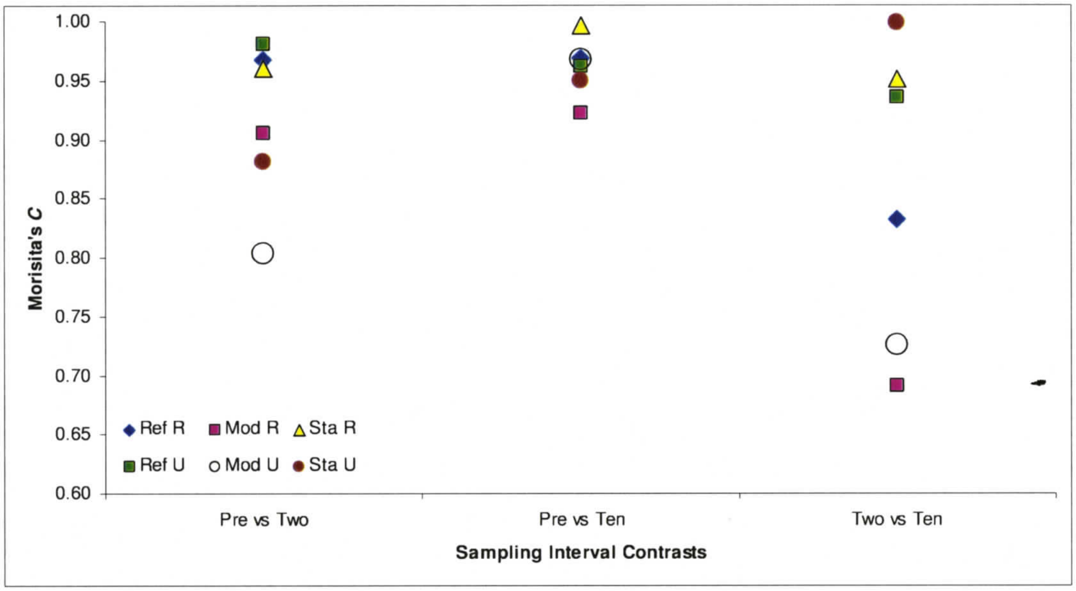


Figure 2-5. Amphibian community similarity coefficients (Morisita's *C*) for each transect contrasted against sampling interval. Pre = pre-harvest (1992-93); Two = 1st post-harvest (1005-96); Ten = 2nd post-harvest (2003-04). Ref = reference; Mod = modified; Sta = State; R= riparian; U = upland.

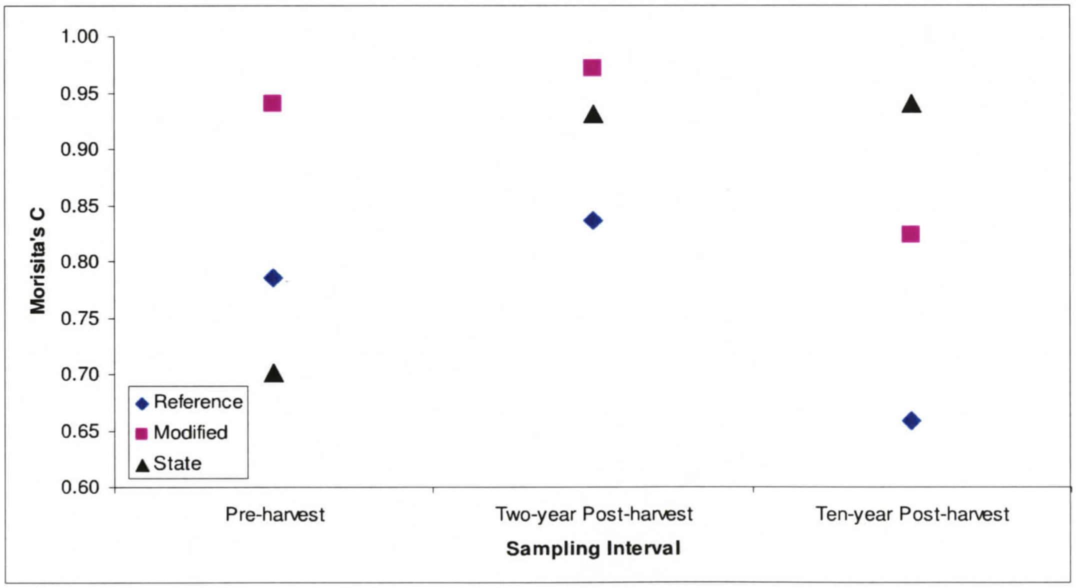


Figure 2-6. Amphibian community similarity coefficients (Morisita's *C*) for comparisons of riparian and upland communities for each treatment within each sampling interval.

Relative Abundance

The total catch for the pre-harvest and two- and ten-year post-harvest periods was 605, 869, and 409 individuals, respectively (Table 2-6). In each sampling period, the total catch was dominated by Western Red-backed Salamanders, Ensatinas, and Tailed Frogs. Overall, these three species constituted 80.9% of all animals captured, with Western Red-backed Salamanders making up 48.1%, Ensatinas 24.6% and Tailed Frogs 7.9%. During the pre-harvest sampling interval, 78.8% of the sample consisted of these three species, 88.7% during the two-year post-harvest sampling interval, and 67.9% ten-years after logging. Within each sampling interval, Western Red-backed Salamanders were the most abundant species captured on riparian transects in all three sampling intervals and on upland transects during the two-year post-treatment interval (Table 2-7). During the pre-treatment and ten-year post-harvest intervals, Ensatinas were the most abundant amphibian captured on upland transects. Some of the less common species captured included Western Toad, Cascade Frog, and Cascade Torrent Salamander, all of which comprised less than 1% of the total sample.

The temporal changes in relative abundance were inconsistent among species and most changes were species-specific. The only species with a significantly higher abundance on one of the transects was Ensatina, which was consistently more abundant in upland transects in all 3 sampling intervals (pre-harvest; $p < 0.01$. two-year post-harvest; $p < 0.01$, and ten-year post-harvest; $p < 0.01$, respectively (Table 2-7). Western Red-backed Salamanders were slightly ($p = 0.07$) more abundant on upland transects during the two-year post-harvest sampling interval. Conversely, the number of the Pacific Giant Salamanders was marginally higher ($p = 0.07$) on riparian transects compared to uplands (Table 2-7).

Table 2-6. Proportion of total captures per transect and treatment for each species caught during each sampling interval for the period 1992 – 2004.

	Pre-harvest (1992-93)						Two-years Post-harvest (1995-96)						Ten-years Post-harvest (2003-04)					
	Reference		Modified		State		Reference		Modified		State		Reference		Modified		State	
Species	R	U	R	U	R	U	R	U	R	U	R	U	R	U	R	U	R	U
Ambystoma gracile	0.08	0.05	0.06	0.10	0.03	0.07	0.04	0.04	0.05	0.00	0.01	0.01	0.11	0.10	0.16	0.04	0.04	0.03
A. macrodactylum	0.04	0.00	0.05	0.01	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.06	0.01	0.00	0.00
Ascaphus truei	0.19	0.14	0.05	0.06	0.06	0.09	0.09	0.17	0.03	0.04	0.04	0.01	0.22	0.14	0.03	0.03	0.09	0.00
Bufo boreas	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Dicamptodon tenebrosus	0.03	0.01	0.04	0.03	0.14	0.01	0.04	0.01	0.01	0.00	0.06	0.00	0.04	0.05	0.06	0.00	0.02	0.00
Ensatina eschscholtzii	0.13	0.48	0.14	0.34	0.08	0.40	0.13	0.35	0.06	0.15	0.09	0.31	0.06	0.40	0.06	0.31	0.14	0.33
Hyla regilla	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00
Plethodon dunni	0.03	0.00	0.01	0.00	0.01	0.00	0.05	0.01	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
P. vehiculum	0.46	0.33	0.42	0.36	0.56	0.35	0.61	0.37	0.66	0.75	0.75	0.62	0.35	0.19	0.22	0.34	0.56	0.52
Rana aurora	0.04	0.00	0.12	0.06	0.10	0.07	0.01	0.05	0.16	0.04	0.03	0.00	0.17	0.04	0.22	0.07	0.07	0.03
R. cascadae	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhyacotriton cascadae	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
R. keezeri	0.01	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.02	0.00	0.04	0.05	0.03	0.03	0.02	0.08
Taricha granulosa	0.00	0.00	0.10	0.04	0.03	0.02	0.02	0.01	0.00	0.01	0.00	0.03	0.02	0.01	0.14	0.16	0.07	0.00
Total Captures	78	128	81	123	72	123	103	189	88	138	114	237	54	97	69	68	57	64
Sampling Interval Totals			605						869						409			

Table 2-7. Abundance rankings of terrestrial amphibians based on raw captures during all three sampling intervals. P-values indicate differences between total riparian and upland captures for each species. Values in bold are significant at α = 0.05, and those and with an asterisk are marginally significant. Rip = Riparian; Upl = Upland; Tot= both riparian and upland.

Pre-Treatment (1992 & 1993): All sites combined					**Sites**		**Riparian**		**Upland**		
Species Code	**Rank**	**Total**	**%**	**Rip**	**Upl**	**Tot**	**Captures**	**%**	**Captures**	**%**	***p***
Plethodon vehiculum	1	239	39.5	18	13	18	110	47.6	129	34.5	0.87
Ensatina eschscholtzii	2	179	29.6	8	16	16	27	11.7	152	40.6	**<0.01**
Ascaphus truei	3	59	9.80	10	8	10	23	10.0	36	9.60	0.29
Ambystoma gracile	4	39	6.40	8	8	11	13	5.60	26	7.00	0.27
Rana aurora	5	35	5.80	8	4	9	20	8.70	15	4.00	0.42
Dicamptodon tenebrosus	6	21	3.50	9	4	10	15	6.50	6	1.60	0.10
Taricha granulosa	7	17	2.80	5	4	6	10	4.30	7	1.90	0.84
Totals		**605**		**11**	**10**	**12**	**231**		**374**		

2 Yr Post-Treatment (1995 & 1996): All sites combined					**Sites**						
Species Code	**Rank**	**Total**	**%**	**R**	**U**	**Tot**	**Riparian**	**%**	**Upland**	**%**	***p***
Plethodon vehiculum	1	526	60.5	18	17	18	207	67.6	319	56.7	**0.07***
Ensatina eschscholtzii	2	189	21.7	10	18	18	28	9.20	161	28.6	**<0.01**
Ascaphus truei	3	56	6.40	6	8	10	17	5.60	39	6.90	0.22
Ambystoma gracile	4	33	3.80	6	5	8	18	5.90	15	2.70	0.49
Rana aurora	5	20	2.30	7	7	10	10	3.30	10	1.80	1.00
Dicamptodon tenebrosus	6	14	1.60	6	2	7	12	3.90	2	0.40	**0.07***
Taricha granulosa	7	11	1.30	2	4	5	2	0.70	9	1.60	0.15
	Totals	**869**		**12**	**12**	**13**	**306**		**563**		

10 Yr Post-Treatment (2003 & 2004): All sites combined					**Sites**						
Species Code	**Rank**	**Total**	**%**	**R**	**U**	**Tot**	**Riparian**	**%**	**Upland**	**%**	***p***
Plethodon vehiculum	1	140	34.2	15	13	17	66	37.1	74	32.0	0.48
Ensatina eschscholtzii	2	96	23.5	9	15	16	15	8.40	81	35.1	**<0.01**
Ascaphus truei	3	39	9.50	10	5	11	28	15.7	11	4.80	0.92
Ambystoma gracile	4	35	8.60	8	6	10	19	10.7	16	6.90	0.64
Rana aurora	5	34	8.30	5	9	10	17	9.60	17	7.40	0.16
Dicamptodon tenebrosus	6	27	6.60	5	3	5	15	8.40	12	5.20	0.63
Taricha granulosa	7	17	4.20	3	3	3	5	2.80	12	5.20	0.77
Ambystoma macrodactylum	8	12	2.90	5	3	8	7	3.90	5	2.20	0.37
	Totals	**409**		**11**	**11**	**13**	**178**		**231**		

Relative Abundance Within Sampling Intervals

Although the goal of my study was to evaluate the temporal effectiveness of RMZs in providing habitat for terrestrial amphibians, it was important evaluate differences in relative abundance within each sampling interval to determine if any of the temporal changes in relative abundance observed were products of site effects. Of particular interest were differences in relative abundance observed prior to timber harvest between treatments and transects. For example, the relative abundance of Ensatina was higher on upland transects of all treatments compared to riparian transects ($t = 2.8$, $p = 0.002$; Figure 2-7). The relative abundance of Tailed Frogs was marginally higher on riparian transects of the reference treatment compared to both the modified ($F_{1,\,35.70} = 3.17$, $p = 0.083$) and state buffered sites ($F_{1,\,34.50} = 2.92$, $p = 0.096$). On upland transects, Tailed Frogs were slightly more abundant at the reference sites compared to the state buffered sites ($F_{1,\,34.50} = 3.42$, $p = 0.072$). Pacific Giant Salamanders were more abundant on riparian transects of the state buffered sites compared to both the modified buffered sites ($F_{1,\,155.0} = 3.23$, $p = 0.074$) and reference sites ($F_{1,\,155.1} = 4.72$, $p = 0.031$). Finally, the relative abundance of Red-legged Frogs was higher at the state and modified buffered sites compared to the reference sites on both riparian and upland transects, but these differences were not significant (riparian: $F_{1,\,68.79} = 1.3$, $p = 0.26$; upland: $F_{1,\,68.79} = 1.8$; $p = 0.18$). The relative abundance of all other species did not vary significantly among treatments or transects prior to harvest (Figure 2-7). The pre-existing differences in relative abundance were considered when determining possible treatment effects.

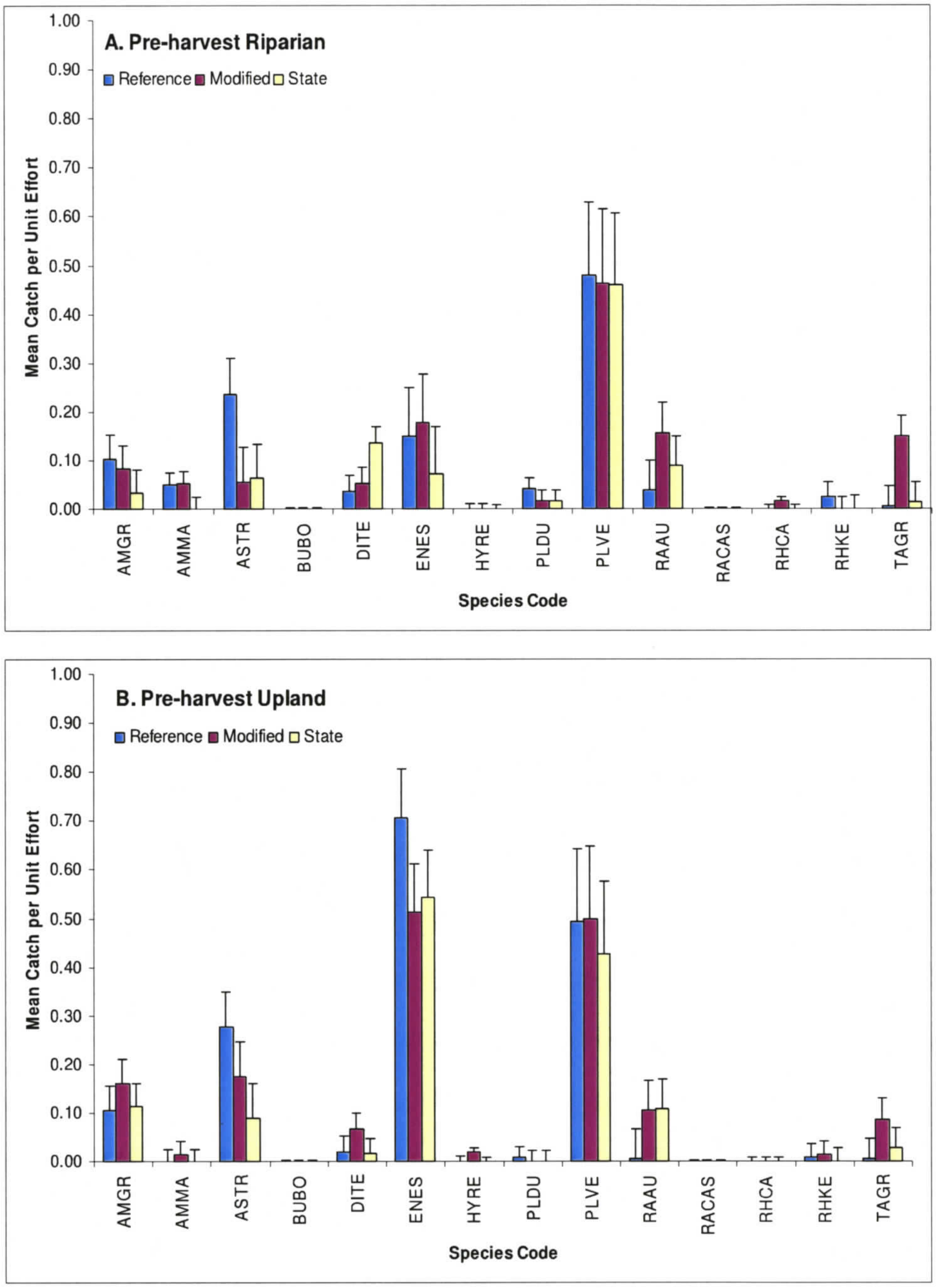
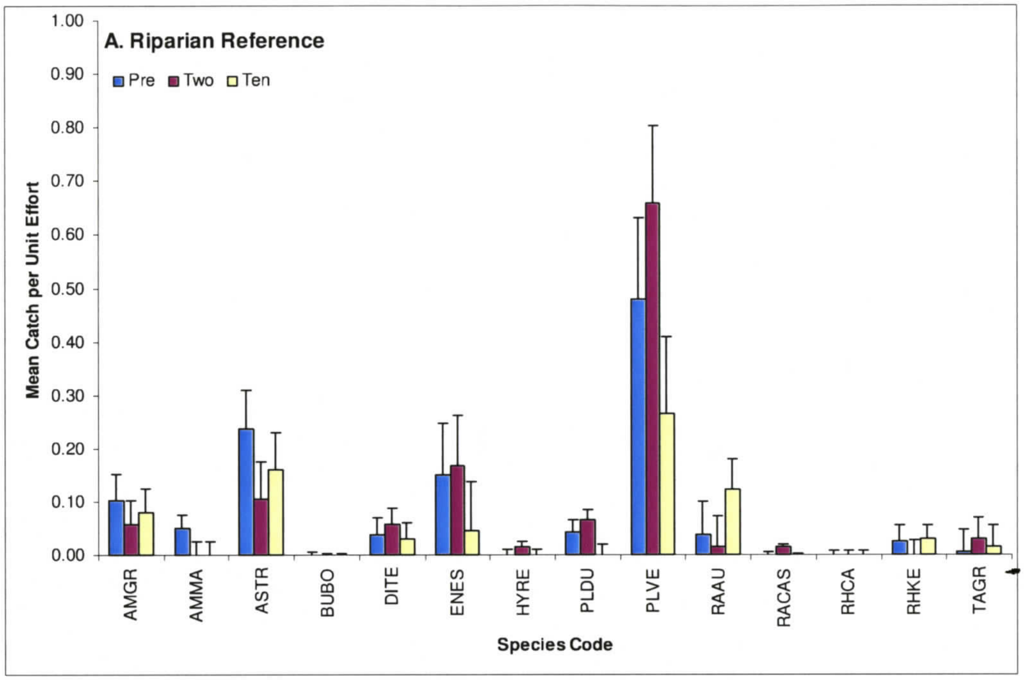


Figure 2-7. Mean catch per unit effort (+SE) (A = Riparian; B = Upland) for each species of terrestrial amphibian caught at the western Washington reference sites during the pre-harvest sampling period (1993-94). AMGR = *Ambystoma gracile*; AMMA = *A. macrodactylum*; ASTR = *Ascaphus truei*; BUBO = *Bufo boreas*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; HYRE = *Hyla regilla*; PLDU = *Plethodon dunni*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; RACAS = *R. cascadae*; RHCA = *Rhyacotriton cascadae*; RHKE = *R. keezeri*; TAGR = *Taricha granulosa*.

Natural Variation at the Reference Sites

One of the functions of the reference group is to allow for an interpretation of naturally occurring changes in the relative abundance of amphibians over time. The mean numbers of animals captured in riparian and upland reference sites were plotted by species for each of the three sampling intervals (Figure 2-8A, B). From these plots, it is evident that large changes in relative abundance occurred for some species but not others. Changes in the relative abundance of amphibians on riparian transects were categorized in one of three ways: 1) no change; 2) an increase in the two-year post-harvest sampling interval followed by a decrease, or 3) a decrease followed by an increase ten years after logging. The relative abundance of Long-toed Salamander, Western Toad, Pacific Treefrog, Cascade Frog and Cascade Torrent Salamander either did not change over time or the species occurred in such low numbers that statistical comparisons were not meaningful (Figure 2-8A). The relative abundance of five species (Pacific Giant Salamander, Ensatina, Dunn's Salamander, Western Red-backed Salamander, and Rough-skinned Newt) increased in the first post-harvest sampling interval then decreased ten years following logging (Figure 2-8A). Only the relative abundance of Western Red-backed and Dunn's Salamanders changed significantly. Western Red-backed Salamanders increased by approximately 30% immediately after logging followed by a 62% reduction ten years later (Figure 2-8A).



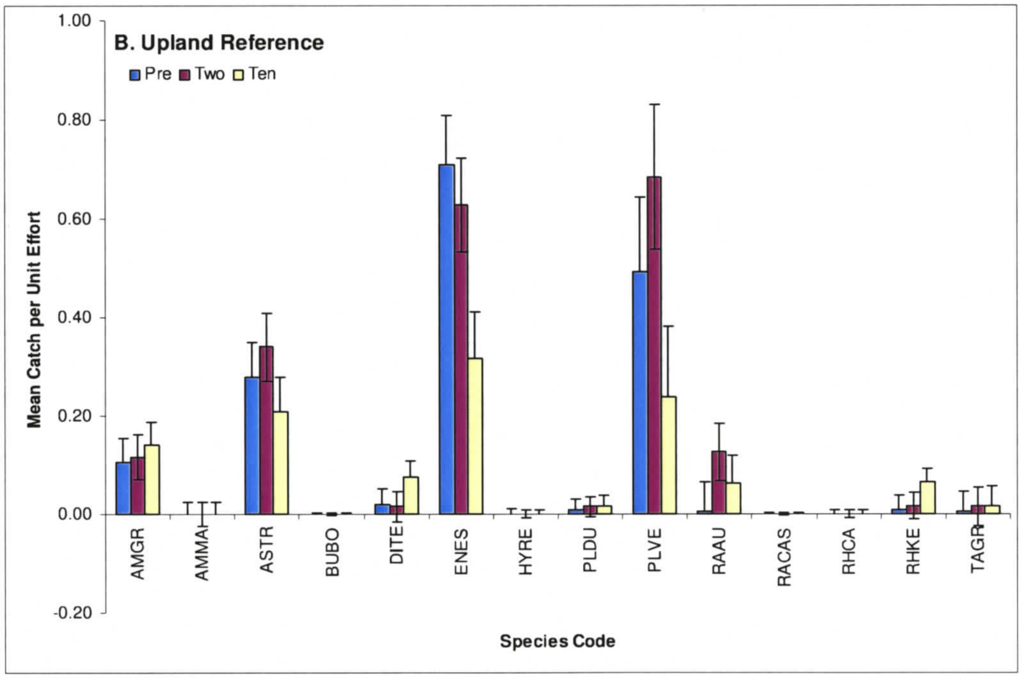


Figure 2-8. Mean catch per unit effort (+SE) (A = Riparian; B = Upland) for each species of terrestrial amphibian caught at the western Washington reference sites during the 1993 – 2004 sampling period. Pre = 1992 & 1993; Two = 1995 & 1996; Ten = 2003 & 2004. AMGR = *Ambystoma gracile*; AMMA = *A. macrodactylum*; ASTR = *Ascaphus truei*; BUBO = *Bufo boreas*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; HYRE = *Hyla regilla*; PLDU = *Plethodon dunni*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; RACAS = *R. cascadae*; RHCA = *Rhyacotriton cascadae*; RHKE = *R. keezeri*; TAGR = *Taricha granulosa*.

The increase in relative abundance of Western Red-backed Salamanders immediately following logging was not significant, but the decrease ten years later was (increase: $F_{1,\ 154.9} = 1.8$, $p = 0.18$; decrease: $F_{1,\ 154.0} = 9.7$, $p = 0.002$). Similarly, the relative abundance of Dunn's Salamanders increased by 33% immediately after logging ($F_{1,\ 154.0} = 0.85$, $p = 0.36$) and decreased significantly ten years later ($F_{1,\ 151.5} = 7.81$, $p = 0.005$). Conversely, numbers of Northwestern Salamanders, Tailed Frogs, Red-legged Frogs, and Columbia Torrent Salamanders decreased in the first post-harvest sampling interval, then increased ten years following logging (Figure 2-8A). Of these species, only the 56.5% decrease in the relative abundance of Tailed Frogs immediately following logging was significant ($F_{1,\ 156.0} = 4.9$, $p = 0.03$).

The patterns of change were more variable on upland transects. Relative abundance either did not change, increased or decreased during both post-harvest sampling intervals, increased in the first post-harvest sampling interval then decreased ten years later, or first decreased then increased (Figure 2-8B). The relative abundance of seven species (Long-toed Salamander, Western Toad, Pacific Treefrog, Dunn's Salamander, Cascade Frog, Cascade Torrent Salamander, and Rough-skinned Newt) did not change, or they were captured in such low numbers that statistical comparisons were not meaningful. The relative abundance of two species (Northwestern Salamander and Columbia Torrent Salamander) increased in both post-harvest sampling intervals. For both species, the increases in relative abundance recorded for the first post-harvest sampling interval were not significant (Northwestern: $F_{1,\ 170.3} = 0.02$, $p = 0.86$; Columbia Torrent: $F_{1,\ 169.3} = 0.05$, $p = 0.81$). The increases measured ten years following logging were not significant for Northwestern Salamanders ($F_{1,\ 169.5} = 0.17$, $p = 0.67$), but were marginally significant for Columbia Torrent Salamanders ($F_{1,\ 168.9} = 3.20$, $p = 0.07$). Ensatina was the only species that consistently decreased in numbers over time (Figure 2-8B), decreasing first by 10% ($F_{1,\ 156.7} = 0.6$, $p =$

0.46) in the first post-harvest sampling interval followed by an additional 50% decrease ten years later ($F_{1,\ 154.9} = 9.21$, $p = 0.002$). The mean relative abundance recorded ten years following logging was significantly lower than the pre-harvest means ($F_{1,156.7} = 13.1$, $p < 0.001$).

The relative abundance of Western Red-backed Salamanders, Tailed Frogs, and Red-legged Frogs increased immediately after harvesting, followed by a decrease ten years later. The relative abundance of Western Red-backed Salamanders and Tailed Frogs increased by 29.2% and 18.2%, respectively, relative to pre-harvest values, which was not significant for either species (Western Red-backed: $F_{1,\ 154.9} = 2.04$, $p = 0.15$; Tailed Frogs: $F_{1,\ 156.0} = 1.08$, $p = 0.30$). The relative abundance of Red-legged Frogs increased marginally ($F_{1,\ 169.6} = 3.21$, $p = 0.07$) in the first post-harvest sampling interval. Ten years following logging the relative abundance of Western Red-backed Salamanders had decreased by 66% ($F_{1,\ 154.0} = 12.4$, $p < 0.001$), Tailed Frogs by 39% ($F_{1,\ 154.7} = 5.4$, $p = 0.02$) and Red-legged Frogs by 50% compared to the two-year post-harvest means ($F_{1,\ 169.1} = 1.02$, $p = 0.31$). Finally, the relative abundance of Pacific Giant Salamanders decreased in the first post-harvest sampling interval, then increased ten years later. Neither the initial decrease ($F_{1,\ 171.4} = 0.005$, $p = 0.94$) nor the subsequent increase ($F_{1,\ 169.8} = 2.17$, $p = 0.14$) were significant.

Riparian Habitats of Buffered Treatments

The relative abundance of terrestrial amphibians clearly changes over time and these changes were species–specific and could be loosely categorized (see previous section). The efficacy of the modified and state buffered sites in providing habitat to maintain relative abundance of terrestrial amphibians (relative to the reference sites) in riparian habitats was evaluated by plotting the change in mean relative abundance (+ SE) for each sampling interval for each buffered treatment (Figure 2-9A, B).

The changes in relative abundance observed on the modified and state buffered sites cannot be categorized as easily as they were for the reference sites. Only the changes in relative abundance of Northwestern and Western Red-backed Salamanders followed a consistent pattern among all three treatments (Figure 2-8; Figure 2-9). The relative abundance of Northwestern Salamanders decreased immediately following logging then increased ten years later at both the state and modified buffered sites. The decrease immediately following logging was not significant for either treatment, nor was the increase on state buffered sites; however, the increase on the modified buffered sites was significant ($F_{1,\ 172.4} = 4.23$, $p = 0.040$). The changes observed at the buffered sites paralleled those observed at the reference sites, suggesting that the width of the riparian buffer did not influence the relative abundance of this species. Western Red-backed Salamanders also changed consistently over time with a large increase in relative abundance in the first post-harvest sampling interval followed by a decrease 10 years later (Figure 2-8 and Figure 2-9). The changes in relative abundance were significant for both sampling intervals at both the state buffered sites (increase: $F_{1,\ 154.5} = 7.1$, $p = 0.008$; decrease: $F_{1,\ 154.0} = 11.5$; $p < 0.001$), as was the decrease at the modified buffered sites ($F_{1,\ 157.3} = 4.8$, $p = 0.03$), and all changes were consistent with those observed at the reference sites. This suggests a probable regional effect that was measured over the duration of this study as opposed to a clearcut logging-induced change in relative abundance. For all treatments, the relative abundance of Western Red-backed Salamanders was lower ten years following logging compared to the pre-harvest means, but not significantly.

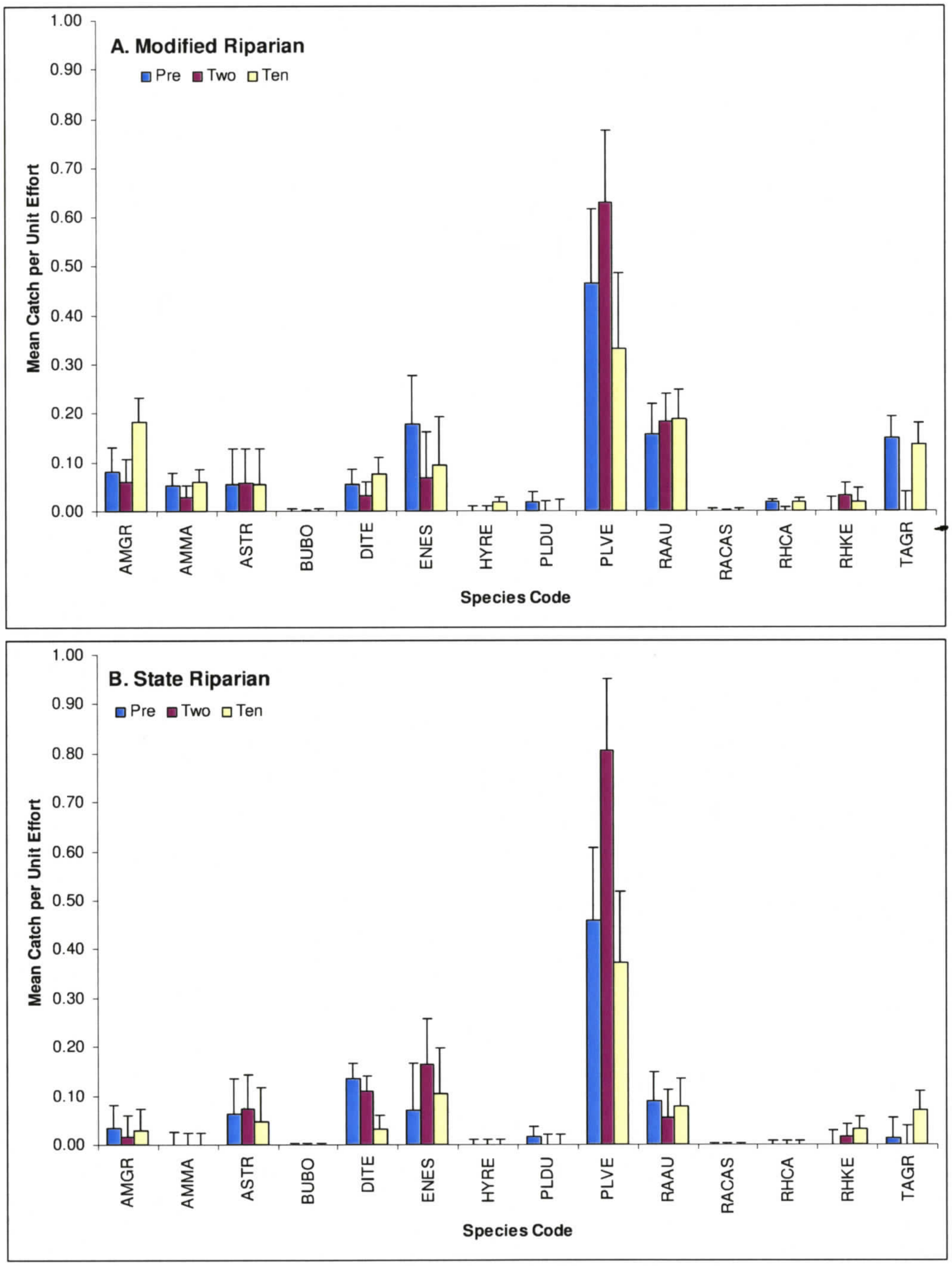


Figure 2-9. Mean catch per unit effort (+SE) (A = modified; B = state) for each species of terrestrial amphibian caught on riparian transects at the western Washington buffered sites during the 1993 – 2004 sampling period. Pre = 1992 & 1993; Two = 1995 & 1996; Ten = 2003 & 2004. AMGR = *Ambystoma gracile*; AMMA = *A. macrodactylum*; ASTR = *Ascaphus truei*; BUBO = *Bufo boreas*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; HYRE = *Hyla regilla*; PLDU = *Plethodon dunni*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; RACAS = *R. cascadae*; RHCA = *Rhyacotriton cascadae*; RHKE = *R. keezeri*; TAGR = *Taricha granulosa*.

Trends in relative abundance were variable for the remaining species and inconsistent among treatments. For example, the relative abundance of Ensatina decreased at the modified buffered sites immediately after logging, but increased at state buffered sites, a change that was consistent with the reference sites, but neither change was significant. Ten years following logging, Ensatina decreased on state buffered sites, again consistent with the reference treatment, but increased at the modified buffered sites. None of the changes were significant and the changes observed for Ensatina exemplify the situation for most species: change in relative abundance was variable and independent of treatment type. The one exception to this was the Pacific Giant Salamander. At modified buffered sites, this species decreased following logging, but increased ten years later; neither of the changes were significant (decrease: $F_{1,\ 171.5} = 0.28$; $p = 0.59$; decrease: $F_{1,\ 174.1} = 1.1$; $p = 0.30$). Similarly, the relative abundance of this species decreased following logging on the state buffered sites by 23% and decreased a further 70% ten years later. The change from the two-year to the ten-year post-harvest sampling interval was marginally significant ($F_{1,\ 169.8} = 3.6$, $p = 0.06$) with the overall reduction in relative abundance ten years following logging significantly different from the pre-harvest means ($F_{1,\ 170.7} = 6.1$, $p = 0.01$).

For species with enough captures to make meaningful statistical comparisons (Northwestern Salamanders, Tailed Frogs, Pacific Giant Salamanders, Ensatina, Western Red-backed Salamanders, Red-legged Frogs, and Rough-skinned Newts), the buffered treatments functioned to preserve relative abundance at levels similar to, or consistent with, the reference sites. Again, the only exception was the Pacific Giant Salamander, which appears to have declined steadily at state buffered sites.

Upland Habitats of Buffered Treatments

The relative abundance of five species (Northwestern Salamander, Tailed Frog, Pacific Giant Salamander, Ensatina, and Red-legged Frog) declined over time on upland habitats of the buffered sites and the decline was not always the same at both treatments (Figure 2-10), nor was the change consistent with the change at the reference sites (Figure 2-8B). The only species with consistent changes in relative abundance was the Western Red-backed Salamander. At all treatments, the relative abundance first increased immediately following logging then decreased ten years later, a pattern that was consistent with the changes observed on riparian transects (Figure 2-9). The initial increase in relative abundance was significant at both the state ($F_{1,\ 154.5} = 26.3$, $p < 0.001$) and modified ($F_{1,\ 155.0} = 4.3$, $p = 0.04$) buffered sites. The subsequent decrease in relative abundance was also significant at both buffered treatments (state: $F_{1,\ 154.0} = 27.4$, $p < 0.001$; modified: $F_{1,\ 157.3} = 8.1$, $p = 0.005$). The change in relative abundance of Ensatinas on upland habitats of the modified buffered sites was consistent with the changes observed at the reference sites, decreasing steadily over time, with the decrease immediately after logging marginally significant ($F_{1,\ 156.8} = 3.2$, $p = 0.07$). Mean relative abundance ten years after logging was significantly lower than pre-harvest means ($F_{1,\ 163.7} = 4.3$, $p = 0.04$). On state buffered sites, the relative abundance of Ensatinas first increased significantly immediately following logging ($F_{1,\ 155.9} = 4.4$, $p = 0.04$), then decreased significantly ten years later ($F_{1,\ 154.9} = 20.9$, $p < 0.001$); the ten-year means were significantly lower than the pre-harvest means ($F_{1,\ 155.9} = 5.6$, $p = 0.02$). On state buffered sites, the ten-year post-harvest means were consistent with both the modified buffered and reference sites (i.e., they were lower than the pre-harvest means), suggesting a regional effect rather than a treatment response.

Pacific Giant Salamanders and Tailed Frogs were likely adversely affected by logging at both buffered sites. Both species were documented at the state and modified buffered treatments prior to harvest (Figure 2-10). Immediately after logging numbers of Pacific Giant Salamanders increased slightly at the state buffered sites and this species was not detected at the modified buffered sites. Ten years following logging Pacific Giant Salamanders were not detected in the upland habitats of either treatment, which is contrary to the pattern observed at the reference sites where numbers of Pacific Giant Salamanders increased ten years following logging (Figure 2-8B). Similarly, the relative abundance of Tailed Frogs declined over time on both the state and modified buffered sites (Figure 2-10). The change in relative abundance was not significant at the state buffered sites, but was close to being significant at the modified buffered sites immediately after logging ($F_{1,\ 156.1} = 3.1$, $p = 0.08$). Furthermore, ten years following logging, the relative abundance of Tailed Frogs was significantly lower than the pre-harvest value ($F_{1,\ 161.2} = 7.4$, $p = 0.007$). Although pre-harvest means were lower at the state and modified buffered treatments compared to the reference sites, the temporal effects on the relative abundance of Tailed Frogs were not consistent among treatments, with the ten-year post-harvest means at the reference treatment not significantly different from the pre-harvest means ($F_{1,\ 156.0} = 1.3$, $p = 0.25$).

Logging the uplands at the state buffered sites may have adversely affected the relative abundance of Northwestern Salamanders. This species declined in numbers immediately after logging with the decline continuing ten years later. The immediate post-logging decline was also observed on upland transects of the modified buffer, but not at the reference sites. Although the initial decline at the state buffered sites was not significant, the difference between the ten-year post-harvest means and the pre-harvest values was close to significant ($F_{1,\ 169.9} = 2.86$, $p = 0.092$)

The relative abundance of the remaining species varied relative to treatment and sampling interval. There were no patterns to the changes observed indicating that site effects were likely responsible for some of the change in relative abundance observed in the upland habitats of all treatments.

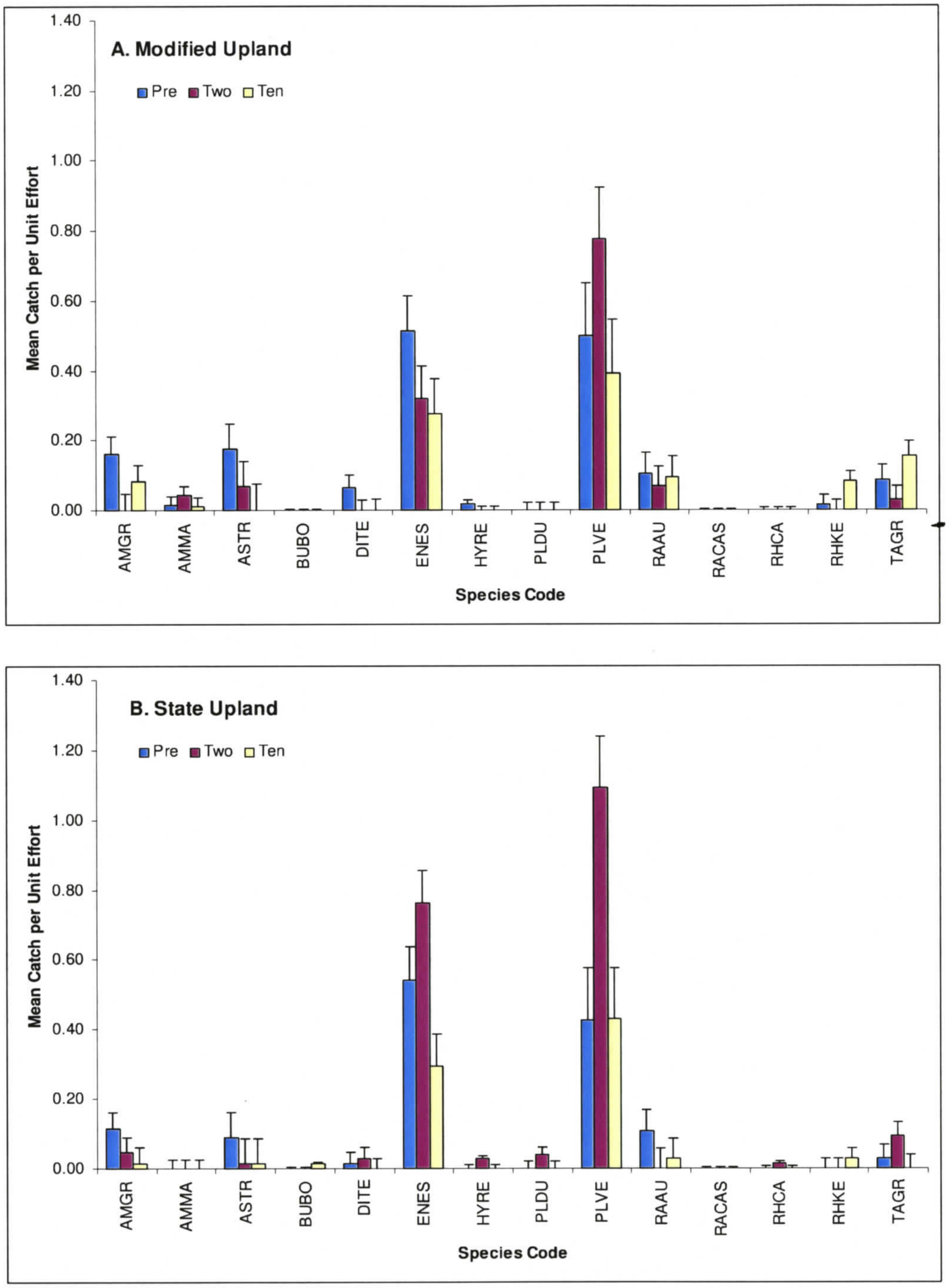


Figure 2-10. Mean catch per unit effort (+SE) (A = modified; B = state) for each species of terrestrial amphibian caught on upland transects at the western Washington buffered sites during the 1993 – 2004 sampling period. Pre = 1992 & 1993; Two = 1995 & 1996; Ten = 2003 & 2004. AMGR = *Ambystoma gracile*; AMMA = *A. macrodactylum*; ASTR = *Ascaphus truei*; BUBO = *Bufo boreas*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; HYRE = *Hyla regilla*; PLDU = *Plethodon dunni*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; RACAS = *R. cascadae*; RHCA = *Rhyacotriton cascadae*; RHKE = *R. keezeri*; TAGR = *Taricha granulosa*.

Discussion

This study provides a measure of the short- (two-year) and medium-term (ten-year) responses of terrestrial amphibian populations to the effects of logging of second-growth forest. It also evaluates and compares the efficacy of riparian buffer widths for their ability to continue to provide habitat attributes necessary to maintain the diversity and abundance of terrestrial amphibians over time. My findings suggest that there is no global response by terrestrial amphibians to logging, or to the retention of riparian management zones in the US Pacific Northwest. Rather, species showed individual responses that varied over time and between treatments and transects. The influence of site effects was evident for some species while for others there is some suggestion of treatment effects, but the analyses were confounded by patterns of natural population change at both local and regional scales.

For most species of terrestrial amphibians, the retention of riparian management zones, regardless of width, ameliorated the impacts of clearcut logging, and no differences in relative abundance were attributable to RMZ width. Only the relative abundance of the Pacific Giant Salamander was adversely affected on the state buffered sites, indicating that the narrow buffer width was not effective in maintaining the relative abundance of this species at levels comparable to the pre-harvest means. Moreover, because the relative abundance of this species increased in riparian habitats of the modified buffered sites, the width and configuration of these sites is sufficient to maintain the relative abundance of this species in riparian habitats. This may also be true for Northwestern Salamanders; however, the relationship between relative abundance and buffer width is not as strong.

Logging upland forests has been implicated in the decline of amphibians in the Pacific Northwest (deMaynadier and Hunter 1995; Collins and Storfer, 2003; Karraker and Welsh 2006). However, in my study, I found no evidence to suggest that logging directly affected the species richness or community similarity of amphibians, and for most species, changes in relative abundance were not directly related to logging. Two species (Pacific Giant Salamanders and Tailed Frogs) were negatively affected by logging of the uplands and neither the state nor modified buffered RMZ was able to offset the impacts on relative abundance. Both species were either absent, or their relative abundance was significantly lower on upland habitats of the state and modified buffered sites two and ten years following logging relative to the pre-harvest values. For Pacific Giant Salamanders, their absence from upland habitats was associated with significant declines in the riparian habitats of the state buffered sites. The relative abundance of Tailed Frogs was not affected in riparian habitats of either buffered treatment, suggesting that persistence of Tailed Frogs in riparian forest is not directly tied to riparian buffer width or to higher canopy cover values in the adjacent upland forest. However, logging of uplands may have limited the dispersal of this species into upland habitat two and ten years after logging, a trend that has been reported elsewhere (e.g., Ashton et al. 2006; Dupuis and Steventon 1999; Corn and Bury 1989).

The non-detection of Pacific Giant Salamanders in upland habitats of the harvested sites is likely related to the effects of logging on the movement patterns of this species. Johnston and Frid (2002) found that logging restricted the movement patterns of Pacific Giant Salamanders and that after logging, salamanders remained significantly closer to the stream, spent more time in subterranean refuges, and had smaller home ranges than those in forested sites. Johnston and Frid (2002) also found that movement of Pacific Giant Salamanders in riparian buffers was similar to that observed in forested sites and significantly different from clearcut sites. My findings corroborate this: the mean relative abundance of Pacific Giant Salamanders was higher in riparian buffers compared to upland habitats of harvested sites and not markedly different for riparian buffers compared to the upland habitats of reference sites. Over time, the relative abundance of this species remained higher on upland habitats at reference sites where salamanders presumably had larger home ranges and were not restricted in their movement.

Not only was the relative abundance of most species not affected by logging or measurably different on either buffered treatment, RMZ width was not associated with increased or different species richness or community similarity. In general, it appears that riparian buffer width or even logging did not affect the persistence of common species at each treatment group, which is contrary to some literature (Vesely and McComb 2002) and congruent with other literature (Raphael 1991). In the Vesely and McComb (2002) study, sites were not repeatedly sampled across time to remove potential site effects, which could have confounded the interpretation of their results. In fact, most studies evaluating the effects of forestry management on amphibian richness and abundance data have not been well replicated, did not resample the same sites before and after logging (and therefore could not account for site effects), and reported on data collected over a relatively short time period (see reviews in deMaynadier and Hunter [1995] and Cushman [2006]).

The consistent change in the relative abundance of Western Red-backed Salamanders at all treatments and transects and the decline in relative abundance of Ensatinas on upland transects of all three treatments provide examples of how regional population change could potentially confound the interpretation of my data. A regional change in populations of Ensatina was evidenced by a decline in relative abundance at the reference sites. Bury and Corn (1988) reported a significant positive correlation between Ensatina and advanced decay class logs and coarse woody debris. They also reported that Ensatina were more abundant in young forests (30 – 76 years) compared to intermediate-aged stands. In this study, the decline of Ensatina does not appear to be related to any particular habitat feature that is missing from the landscape. Rather it is probable that I observed an expected decline in this species due to forest succession.

Forest communities develop through a continuum that, for conceptual purposes, has been grouped into sequential stages (e.g., Thomas 1979; Bunnell et al. 1999). Figure 2-11 depicts six seral (structural) stages of forest succession as they are conceptualized for a forest stand culminating in an old-growth climax. Stage 1 begins with a vegetation community dominated by non-woody plants such as rushes, grasses, and forbs. By stage 2, woody shrubs and shade-intolerant conifer seedlings are present. At stage 3, conifers begin to dominate the site as they compete for light, water and nutrients with other plants. During stage 4 the conifer canopy closes, effectively shading out vegetation on a forest floor that is becoming increasingly barren. At stage 5, conifers are mature and weaker trees begin to die. Those trees will stand as snags that will eventually fall to the forest floor where they become coarse woody debris. Shade-tolerant species of conifers become established in the understory. During stage 6, shade-intolerant species of conifers are gradually out-competed by the shade-tolerant ones. Those shade-tolerant ones continue to germinate and grow up in the understory. The number of standing dead trees and downed logs increases. Dead and fallen trees create gaps in the canopy that, together with other stand-mediated changes to microclimatic conditions, create suitable conditions for shade-intolerant species. The increasing diversity of plant species and of the density, size, age, and state of decay of those species promotes the structural heterogeneity of the forest during stage 6.

Although species richness did not vary significantly across time, species composition did. The changes in species composition can be partially explained using standard conceptual models. Coniferous forests typically display the pattern of species richness depicted in Figure 2-11. In that pattern, species richness is comparatively higher during the earliest and latest seral stages. As the tree canopy closes (around stage 4), the understory is shaded out, resulting in a decline in habitat suitability for some species. As succession progresses, the structural diversity and richness of plant species in the forest increases. This brings about an improvement in habitat suitability for many species, which in turn facilitates an increase in wildlife-species richness. Although wildlife-species richness in early and late successional stages can be similar and have some species in common, the make-up of the wildlife communities is notably different. In this study, it appears that populations of Ensatina are responding directly to this model of forest succession and one would expect that once the stand reaches old-growth status, the relative abundance of Ensatina on upland habitats would increase – a prediction partially supported by Bury and Corn (1988). If the model depicted in Figure 2-11 is accepted, the relative abundance of Ensatina should be highest in forests between 30 and 80 years of age and older than approximately 250 years with a decline in relative abundance between 80 and 200 years.

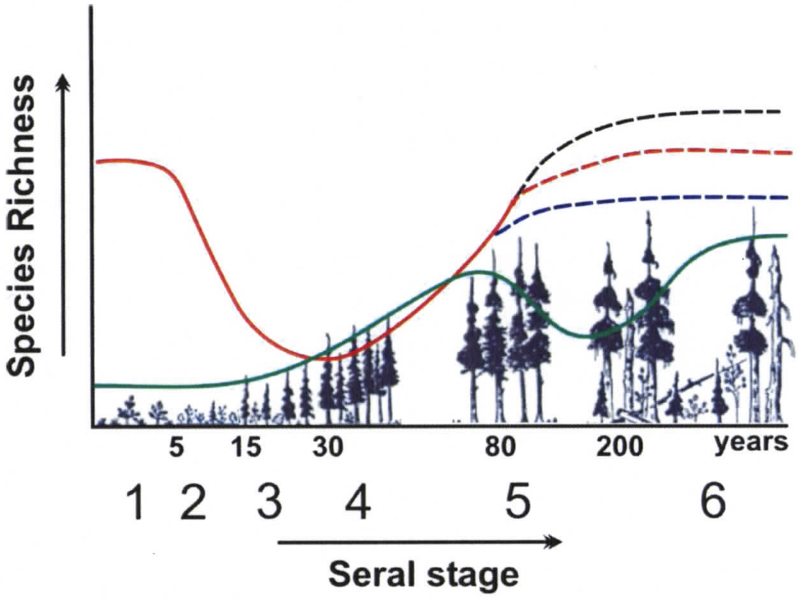


Figure 2-11. Conceptual model of the relative change in species richness (number of species) for wildlife communities as a function of forest seral stage, showing three possible outcomes (dashed lines) of lesser, similar and greater species richness during the earliest and latest stages. The expected relative abundance of Ensatina is shown as a green line. Adapted from Franklin (1990) and Bunnell et al. (1999).

The interpretation of my results is subject to a number of caveats that should be considered for future studies of this type. First, the regional scale of this study represents a dilemma in terms of comparing differences in species richness at the treatment level. This is because not all amphibians in Washington State are ubiquitous or widespread, so there should be differences in species richness that are independent of treatment. For example, certain species (Dunn's Salamander and Columbia Torrent Salamander) are restricted to the southwestern portion of the state (i.e., the Abernathy, Ryderwood 860 & 1557, and Vail Sites; Figure 1-1) whereas other species (e.g., Western Red-backed Salamanders, Ensatina, and Rough-skinned Newts) are ubiquitous in their distribution. Typically, the geographic range of a species does not need to be considered because of the small spatial scale at which most studies are conducted (deMaynadier and Hunter 1995; Cushman 2006). However, for region-wide studies, the inclusion of species that have small geographic ranges can skew the interpretation of species richness data.

Second, accurate differences in species richness would be noted only if all species could be caught using the same capture methods; however, this is not likely to be the case. Mackenzie et al. (2004) point out that many ecological studies evaluating the spatio-temporal patterns of species assume equal detection of all species present. This assumption can lead to incorrect inferences about patterns of species richness because some species may be inaccurately labelled as absent when they simply were not detected. In most cases in my study, the more abundant species were captured at each site (Table 2-8), but even the widely distributed species were not always detected (e.g., *Taricha granulosa*) using the capture methods I employed. Some species of amphibians (e.g., Pacific Treefrog) are not easily captured in pitfall traps, while others (e.g., Larch Mountain Salamanders) may be so patchy in their distribution that even if a site occurred in their expected range, they might not be captured by pitfall trapping. Finally, the behaviour of other species (e.g., Long-toed salamanders) may preclude detection through pitfall trapping. In most studies where pitfall tapping is used as the primary means for species detection, pitfall traps are used in conjunction with drift fences that increase the catchability of the trap (see Heyer et al. 1994). Drift fences were not used in this study, which may have contributed to lower than expected species richness at each site (and treatment) and perhaps to lower relative abundance values.

Table 2-8. Expected versus observed species presence in Western Washington. Shaded cells with bold values indicate that the species was detected at all of the expected sites.

	Sites Expected			SI 1[a]		SI 2[a]		SI 3[a]	
Species	SI 1[a]	SI 2[a]	SI 3[a]	Obs	%	Obs	%	Obs	%
A. gracile	18	18	17	11	61	10	56	11	65
A. macrodactylum	18	18	17	5	28	3	17	2	12
A. truei	18	18	17	8	44	8	44	9	53
B. boreas	18	18	17	1	6	1	6	2	12
D. tenebrosus	13	13	11	11	85	7	54	8	73
E. eschscholtzii	18	18	17	13	72	16	89	15	88
H. regilla	18	18	17	2	11	3	17	2	12
P. dunni	4	4	3	4	**100**	3	75	2	67
P. larselli	4	4	4	0	0	0	0	0	0
P. vandykei	7	7	7	0	0	0	0	0	0
P. vehiculum	18	18	17	16	89	16	89	17	**100**
R. aurora	18	18	17	9	50	9	50	10	59
R. cascadae	13	13	11	0	0	1	8	0	0
Rh. Cascadae	3	3	3	1	33	1	33	1	33
Rh. Kezeri	3	3	3	2	67	2	67	3	**100**
T. granulosa	18	18	17	6	33	6	33	6	35

[a] SI 1 = 1992-93; SI 2 = 1995-96; SI 3 = 2003-04.

Third, to properly assess differences in species richness, sampling needs to coincide with species phenology, employ a variety of capture methods, consider geographic distribution, and consider species density (as a proxy for rarity). Although amphibian species may be active during spring and fall, it is evident that the surface activity of certain species is greater in one season relative to the other and that different capture methods are better for certain species. As an example, spring amphibian data obtained through time-constrained searches and hand-capture from a sub-set of the western Washington study sites in the second post-harvest sampling interval show that in spring, Red-legged frogs were more abundant and more readily detected through time-constrained searches (i.e., hand capture; Figure 2-12) than through fall pitfall trapping. Similarly, although Western Red-backed

Salamanders were the most abundant species detected in the fall in every sampling interval, they represented a larger proportion of the total sample detected in the spring using hand catch methods. To obtain an accurate representation of species relative abundance and species richness, sites should be sampled for amphibians using a combination of methods throughout the year. This will likely increase the species richness and total abundance values.

The utility of sampling sites in different seasons and with different methods to maximize species richness values is exemplified by the number of species detected at the Blue Tick Modified site in the third sampling period. In the spring, five species were detected in riparian habitats whereas only one was documented in the upland for a total of five species at the site. In the fall, four species were detected in the riparian, three in the upland for a total of four species at the site. The richness measure used in this study was derived from only the fall data. If data from both sampling intervals had been combined, the total number of species detected would increase to six. If spring sampling had occurred at all sites, it is likely that different richness values would have been derived for each site, habitat type, and treatment and could potentially influence the results.

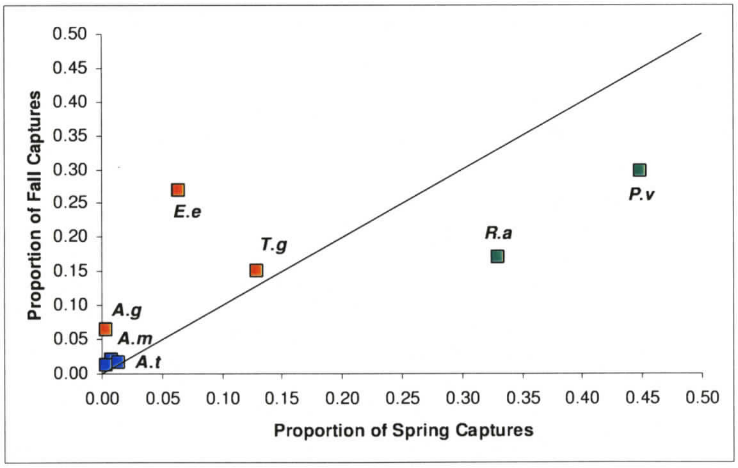


Figure 2-12. Proportional catch of amphibians detected in spring and fall from a subset of sites (n = 6) in Western Washington. *A.g* = *Ambystoma gracile*; *A.m* = *Ambystoma macrodactylum*; *A.t* = *Ascaphus truei*; *E.e* = *Ensatina eschscholtzii*; *P.v* = *Plethodon vehiculum*; *R.a* = *Rana aurora*.

Finally, the use of count data (as a proxy for abundance) and species-richness measures may provide misleading results when evaluating the temporal effects of timber harvest on terrestrial amphibians. Because relationships between counts and abundance are rarely demonstrated, it is difficult to calculate how well counts reflect temporal changes in population numbers. Furthermore, a thorough understanding of population dynamics depends not only on knowing abundance, but also requires knowledge of the fundamentals of population processes, such as survivorship, and it is these we need to study to determine whether and how populations are affected. The collection of pretreatment data, including information on life history parameters and movement patterns, are critical in determining the temporal and spatial responses of terrestrial amphibians to forest harvesting (Maxcy and Richardson 2000). The generally limited dispersal and movement capabilities of many terrestrial amphibians, particularly terrestrial salamanders, may be further inhibited following large-scale habitat perturbations like clearcut logging, which may contribute to any effects of forest harvest on these species (Stebbins 1954; Ovaska, 1988; Grialou et al. 2000). An understanding of home range size and seasonal habitat use prior to logging would also help elucidate the effects of logging on terrestrial amphibians.

Several studies have suggested that buffers wider than those used in this study would be beneficial to amphibians. McComb et al. (1993) reported that a buffer width of 50 m adjacent to second and third order streams in Oregon would provide marginal habitat suitability for amphibians and buffers should be > 50 m wide to provide linkages between mature forests. Vesely and McComb (2002) estimated that RMZs 43 m wide would be sufficient to maintain the relative abundance of amphibians and buffers of 47 m would support species richness at levels similar to unlogged sites. Recently, Crawford and Semlitsch (2007) found that a buffer width of 27 m would support 95% of the salamander species at a site and that an additional 50 m would ameliorate for edge effects. They recommended that a total buffer of 92.6 m be used in southern Appalachian streams to maintain the biodiversity of salamanders. The minimum buffer width required to preserve the diversity and relative abundance of amphibians is related to geography. I found that the retention of riparian buffer zones of either 14 m (state buffered) or 30 m (modified buffered) around third and fourth order streams in western Washington preserved species richness and diversity of terrestrial amphibians and some species of semi-aquatic amphibians. In general, the 14 m wide buffers were adequate in maintaining the relative abundance of most species. In contrast, 30 m wide buffers always preserved the relative abundance of all terrestrial and semi-aquatic amphibians assessed, suggesting that for the preservation of species richness, community similarity, and relative abundance, the modified buffer out-performed the state buffer. The modified buffer configuration and associated habitat characteristics (i.e., the prescription) serve as a better model for habitat mitigation strategies in forested landscapes of the Pacific Northwest and will likely aid in the preservation of biodiversity. The variability of the modified buffer, both in terms of width and habitat characteristics, and the variability in species distribution and sensitivity to habitat change, dictate that RMZ delineation occur at a scale commensurate with the variability. For example, sites with lower species diversity and lacking sensitive species (i.e., those affected by habitat change) could have a riparian buffer that differs from a site with high species diversity and sensitive species. An understanding of the diversity and distribution of amphibians in western Washington would be invaluable when managing for amphibian biodiversity using riparian management zones.

Chapter 3
Co-inertia Analysis and the Elucidation of Terrestrial Amphibian Habitat Relationships

Introduction

On a global scale, current extinction rates of plants and animals are estimated to be up to 1000 times greater than rates inferred from the fossil record (Wilson 1999; Ballie et al. 2004) and amphibians are among the taxa most threatened with extinction (Stuart et al. 2004; Beebee and Griffiths 2005; Cushman 2006). Amphibians are vulnerable to higher rates of extinction for several reasons: 1) relatively low vagilities, which may amplify the effects of habitat fragmentation; 2) increased mortality risk associated with migration to and from breeding ponds, combined with an increasing proportion of habitat with lowered suitability on the landscape; 3) narrow habitat tolerances, which exacerbates the effects of habitat loss; and 4) a vulnerability to pathogens, increased UV-B exposure, and environmental pollution (Houlahan et al. 2000; Carr et al. 2002; Cushman 2006).

Our ability to infer population-level impacts of habitat alteration on terrestrial amphibians is confounded by the fact that many populations of terrestrial amphibians exhibit significant temporal variability in population size, and by our generally imprecise knowledge of their dispersal patterns (Cushman 2006). Furthermore, McGarigal and Cushman (2002) found that few amphibian studies have been conducted at the landscape level, resulting in a greatly reduced ability to associate population-level changes with changes in habitat structure or quality. Moreover, effective conservation of amphibian populations is limited by a lack of species-specific ecological knowledge, and a lack of landscape-level studies of the effects of habitat change on movement, survival rates, and population dynamics (McGarigal and Cushman 2002; Cushman 2006).

The incorporation of biodiversity goals into forest management planning requires an understanding of how habitat changes affect the distribution and abundance of species (Patrick et al. 2006). It is also important to understand how habitats change as a result of management strategies that are designed to preserve habitat function and to preserve species diversity and abundance. Implicit in these goals is the need to understand the species-specific habitat relationships of the landscape being managed.

Various statistical methods are available to investigate species-habitat relationships. Direct gradient (or regression), indirect gradient (ordination), and classification (cluster) families of multivariate statistics are popular in community ecology to illuminate relationships between species, genera, or guilds, and available habitat attributes. Classification techniques are discussed by van Tongeren (1995) and comprehensive reviews of gradient analyses are provided by ter Braak (1995), ter Braak and Prentice (1988), and Dray et al. (2003). In general, methods of ordination (including gradient analyses) are multivariate statistical methods designed to analyze ecological data sets over numerous sites.

Forms of gradient analyses include Correspondence Analysis (CA; Gittins 1985) Canonical Correspondence Analysis (CCA; ter Braak 1986), and Redundancy Analysis (RDA; Wollenberg 1977). Most direct gradient methods use iterative optimization techniques to arrange sites along environmental axes based on the species composition and environmental conditions at each site (ter Braak 1987). Nonlinear (unimodal) statistical models are preferable to linear models for species/environment relationships because species abundance usually follows a normal distribution curve along each environmental gradient (ter Braak and Prentice 1988). This is typically the case at regional scales as species ranges can be considered broad-scale response surfaces with survival probability declining away from a central region where the species' ecological intensity (abundance or presence/absence) is highest (Harvey 1996).

Classical methods, like Principal Components Analysis (PCA), aim at summarizing a dataset (e.g., habitat data) by searching orthogonal axes on which the projections of the sampling points have the highest possible variance. This characteristic ensures that the associated factor maps will represent the initial data in the best way (Diallo et al. 2006). Canonical Correspondence Analysis and RDA are multivariate ordination methods that belong to the family of two-table coupling methods (Thiolouse et al. 2004). The intent of these analyses is to interpret relationships between species and environmental variables and not simply to represent numerical relationships among samples or species. Of the various methods of ordination available to describe species-habitat relationships, CCA and RDA are among the most widely used (Dray et al. 2003), yet these methods are not always appropriate when simultaneously analyzing two ecological datasets. Co-inertia Analysis (COIA; Dolédec and Chessel 1994), an alternative to CCA and RDA, is often better suited to the analyses of ecological data despite its relative lack of representation in the literature (Dray et al. 2003). Co-inertia analysis is particularly suited for the simultaneous detection of faunal and environmental features in studies of ecosystem structure because the resulting sample scores of the species and environment data are the most covariant (Dolédec and Chessel 1994; Dray et al. 2003; Diallo et al. 2006).

In ecological studies, sample size is often limiting and this is particularly true for studies that occur at regional scales. In those instances, there is often a tradeoff between cost and replication (Hurlbert 1984; Oksanen 2001). Because of this, the number of samples obtained is often much lower than the number of environmental variables for which data were collected. To apply ordination methods such as CCA or RDA to ecological data, the number of samples must be large relative to the number of environmental variables. This is required because of the inclusion of a regression step in both CCA and RDA that ensures that the sampling scores are linear combinations of the environmental variables (Thiolouse et al.

2004). Co-inertia analysis does not contain a regression step and therefore does not have the constraint of requiring many samples relative to environmental variables. Additionally, RDA and CCA are limited in their application such that RDA should be used only when the species response curve along an environmental gradient is linear, and CCA can be used only when the species response curve is unimodal (Thilouse et al. 2004). In both cases, *a priori* knowledge of the species response curve is required to properly select the method of ordination. Furthermore, because of the regression step involved in CCA, the role of the environmental variables may be underestimated if the number of samples is low. Unlike the more commonly used multivariate analyses, such as CCA, for which the number of environmental variables is limited to the number of sites minus one, COIA has no limitations on the number of environmental variables that can be used, regardless of the number of sites sampled (Thioulouse et al. 2004).

Because COIA can incorporate other multivariate techniques (e.g., principal components analysis and multiple correspondence analysis), it is more flexible than the two current standard techniques (RDA and CCA), which provide only for the modeling of species response curves in a linear or unimodal manner. The ability to model the relationship between species and environmental variables at a regional scale when the number of samples is less than the number of environmental variables makes COIA a more suitable choice. Furthermore, because COIA is a descriptive technique without predictive abilities, it is an appropriate tool to use to explain the relationships between species and habitat attributes measured over time.

Habitat structure influences the occurrence and abundance of terrestrial amphibians (Ash 1988; deMaynadier and Hunter 1995; Aubry 1997) and in many cases, habitats used by terrestrial amphibians are complex, diverse and difficult to characterize, making the potential efficacy of habitat-management strategies difficult to gauge. Habitat loss and fragmentation are among the largest threats to amphibian populations and there have been myriad studies of the impacts of habitat loss or alteration on terrestrial amphibians (Petranka et al. 1993; Knutson et al. 1999; DeGraaf and Yamasaki 2002; Johnston and Frid 2002; Knapp et al. 2003; MacCracken 2004; Goldstein et al. 2005). Studies of the relationship between terrestrial amphibians and habitat attributes have shown that terrestrial amphibians can exhibit positive relationships with increasing forest area (Dupuis and Steventon 1996; Houlahan et al. 2000) or negative relationships with urban development (Delis et al. 1996) and roads (Carr et al. 2002). Kolozsvary and Swihart (1999) describe a general pattern of increased species richness with increasing forest cover. The abundance of amphibians has been shown to decline dramatically in response to environmental stressors such as timber harvesting (Ash 1997; Dupuis 1997; Waldick 1997; deMaynadier and Hunter 1998; this study), but few studies have evaluated how riparian management zones serve to provide habitat for terrestrial amphibians after logging (Biek et al. 2002; Vesely and McComb 2002), or how habitat features retained in riparian management zones function to preserve the diversity and abundance of amphibians.

Objectives

I used COIA to describe habitat associations of terrestrial amphibians in managed forests of western Washington. I was particularity interested in the application of COIA in identifying species-specific habitat relationships that either changed over time because of logging, or that remained consistent within RMZs, which served as an indication of the importance of retaining riparian habitat on the landscape. I also wanted to determine if COIA was capable of identifying patterns of habitat associations based on the coarse-scale habitat data collected at my study sites. Because different RMZ prescriptions were being tested for their efficacy in providing habitat for terrestrial amphibians following logging, I wanted to determine if COIA was sensitive enough to differentiate among treatments within each sampling interval. I anticipated that COIA could provide a visible indication of how each buffered treatment varied across time relative to each other and to the reference sites. Finally, I wanted to determine if some of the changes in relative abundance documented in Chapter 2 could be explained by changes in habitat structure. For example, what was it about the state buffered sites that may have contributed to a decline in the relative abundance of Pacific Giant Salamanders?

Methods

Vegetation and Habitat Structure Sampling

Vegetation sampling occurred once during each sampling interval and coincided with the primary period of productivity and when most plants were identifiable to species, which in this case was summer. Vegetation data from the pre-treatment and two-year post treatment sampling intervals were provided by the Washington Department of Natural Resources. Ten-year post-harvest vegetation data were collected in conjunction with LGL Limited environmental research associates.

Riparian and upland habitats at each site were sampled using a combination of larger and smaller quadrats: 12 in the riparian and 10 in the upland. Sample sites consisted of four 10 X 8 quadrats (Figure 3-1). Riparian quadrats extended 8 and 16 m from the ordinary high water mark, which was usually within 5 m of the stream edge. Upland habitats were sampled in the adjacent upland approximately 100 m upslope from the riparian transect. Within each large quadrat, I established 2 x 2 m and 1 x 1 m plots for the collection of ground cover measurements (Figure 3-2). These smaller plots were located 1, 4, 7, and 10 m from the streamside edge of the large quadrat.

At each quadrat I estimated the percentage cover of herbaceous and woody vegetation, rock, litter, and bare soil at 1, 4, 7, and 10 m from the streamside edge of vegetation quadrats using the 2 X 2 m and 1 X 1 m plots. The percentage cover of shrubs was estimated in quadrats 2 and 3 at each site in the riparian and upland sampling areas. Shrubs were grouped into three categories: 1) berry-producing; 2) evergreen; or 3) other deciduous.

Percentage of downed wood was estimated from quadrats 2 and 3 at each survey site. Wood was considered down if its angle of incidence with the ground was < 45°. Each piece of downed wood was categorized by diameter (cm) (2 classes) and decay class (3 classes) (Table 3-1).

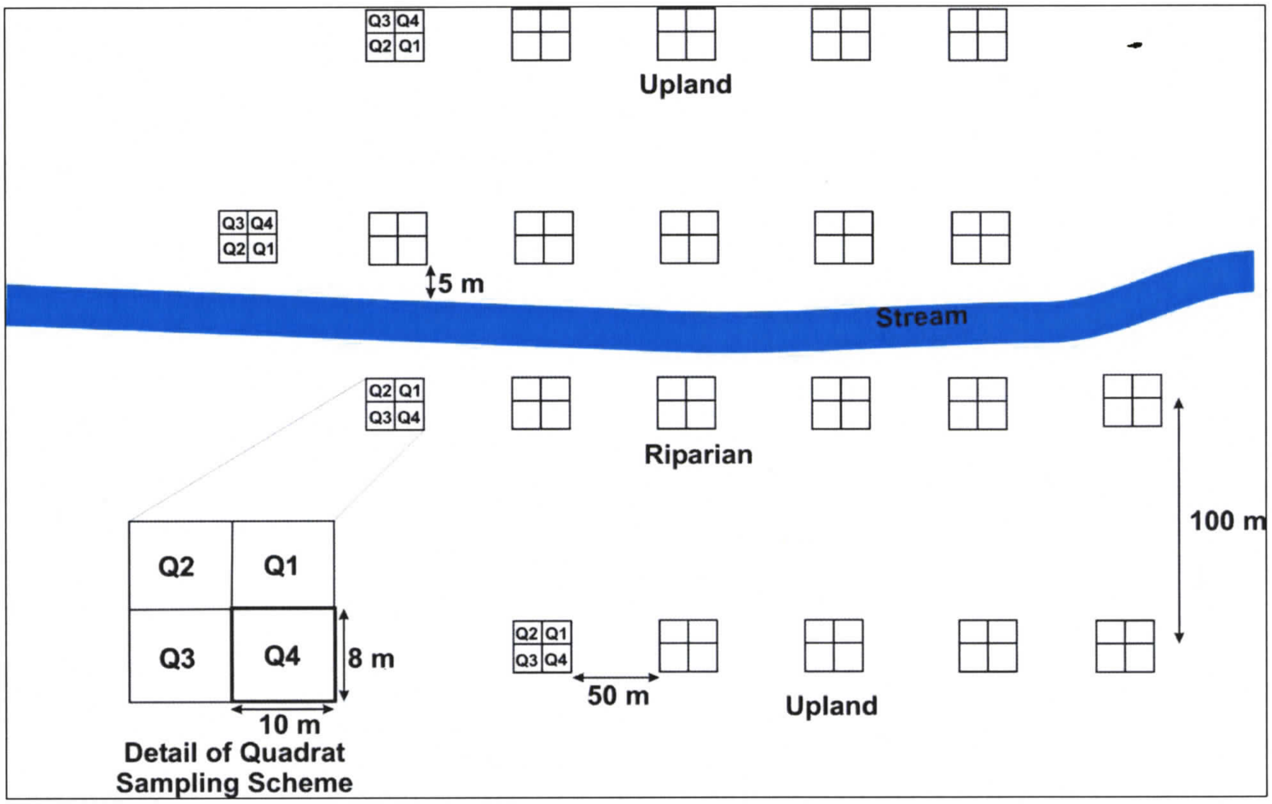


Figure 3-1. Schematic of the vegetation sampling scheme using 10 X 8 quadrats situated on each side of the stream at each study site.

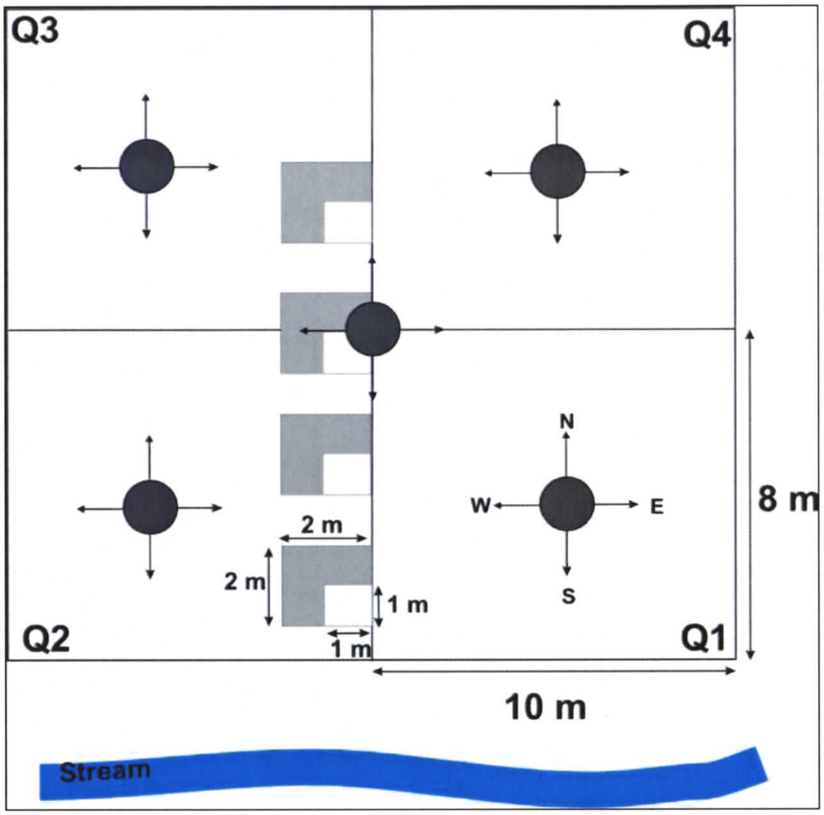


Figure 3-2. Vegetation sampling design schematic showing the location of the 2 X 2 and 1 X 1 m plots at 1, 4, 7, and 10 m from the edge of the quadrat (Q) and the locations from which canopy cover data were collected (black circles).

Table 3-1. Diameter and decay class categories to be used for downed wood measurements in quadrats 2 and 3.

Diameter Class (cm)		Decay Class	
1	10 – 30	1	Structurally sound wood with intact limbs
2	> 30	2	Reduced structural integrity and some limb loss
		3	Minimal structural integrity and presence of epiphytes

Snags were counted in all four quadrats and grouped according to quadrat location. They were classified as short (<1.5 m), medium (1.5 – 15 m) and tall (>15 m) in three diameter classes: Class 1 = all limbs attached and structurally sound; Class 2 = losing limbs and showing reduced structural integrity; and Class 3 = about to fall down due to minimal structural integrity

Percentage cover of sapling trees was estimated from quadrats 2 and 3. Saplings between 1 and 3 m in height were included regardless of whether they originated from the ground, a stump, or downed wood. Each sapling was identified to species and I estimated percentage cover for each species encountered in each quadrat. I did not include tree species in my analyses that were <1 m tall.

In all four quadrats I counted trees > 3 m in height and grouped them according to quadrat (1, 2, 3, or 4) and diameter size (10 cm, 10 – 50 cm, 50 – 100 cm, > 100 cm diameter at breast height (DBH)). I counted all trees with split boles as more than one tree (with the exception of vine maple, *Acer cirinatum*) if the split occurred below breast height. Trees with more than half of the bole outside the quadrat were not counted.

Riparian buffer width was measured from the normal high water mark to the outermost edge of forest and I measured riparian buffer width from five locations on either side of the stream. Slope distance rather than horizontal distance from the outer-most tree to the normal high water mark was measured.

To estimate canopy cover I used a spherical, convex densiometer at the centres of each quadrat and at the centre point where the four quadrats met. At each of the five points, I took four readings: 1) facing the stream; 2) away from the stream; 3) downstream; and 4) upstream (Figure 3-2). I recorded the average canopy cover from each of the five locations in each quadrat.

Other data recorded at each site included air and soil temperature, relative humidity, slope, and aspect.

Co-inertia Analysis

I used R V 2.2.1 (© 2005, The R Foundation for Statistical Computing) to investigate habitat relationships between the relative abundance of common species of amphibians and the habitat attributes measured at each site and treatment. For these analyses COIA was used and was based on the ade4 package available for R (Chessel et al. 2005). Because COIA is a paired ecological table analysis, it requires two datasets, one containing relative abundance X sites data, the other with environmental variables X sites data. Each table was related through a common number of rows, which in this case represented the sites at which data were collected.

Co-inertia analysis relies on the covariance matrix produced from (in my case) a simultaneous PCA of the environmental and species data. Each ecological dataset was first analysed using PCA, which produced two visualizations of the sites in space: one represented by the relative abundance data, the other by the environmental variables data (Figure 3-3). The covariance matrix from each PCA was then joined through a COIA, the output of which was used to visualize how the two initially unrelated datasets co-vary at the same sites.

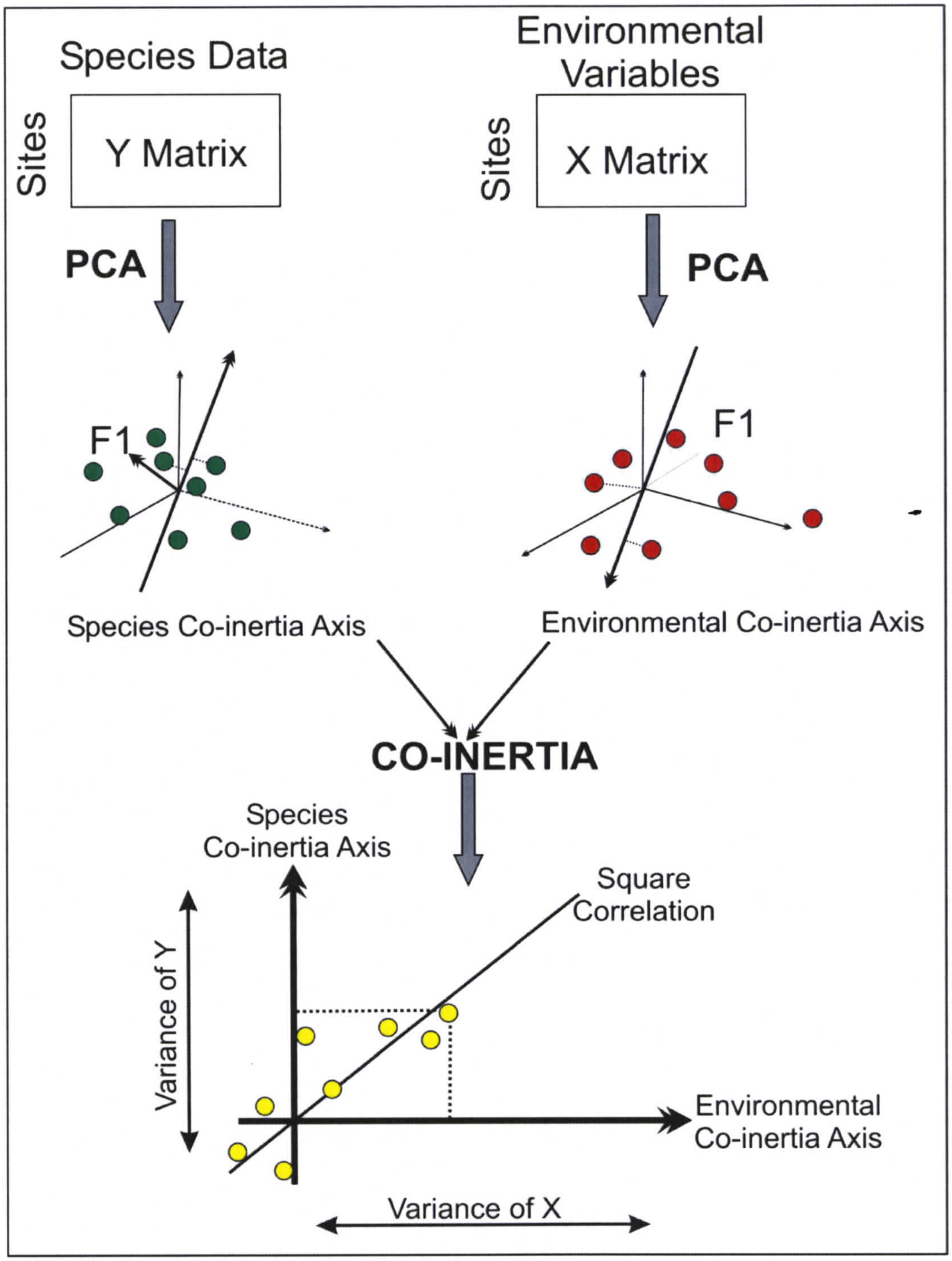


Figure 3-3. Schematic showing the principles of co-inertia analysis. The two ecological data tables X and Y produce two representations of the sites in two hyperspaces. Separate analyses find axes maximizing inertia (= variation) in space (F1 [first factorial axis]). Co-inertia analysis maximizes the square covariance between the projections of the sites on the co-inertia axes (modified from Dray et al. 2003).

The relationship between species' relative abundance and environmental variables can be viewed on a biplot. One approach is to view the species' relative abundance and environmental variable biplots side by side to look for relationships. Alternatively, and as I have done, the species' relative abundance biplot can be superimposed onto the environmental variable biplot for easier interpretation. When this is done, an environmental gradient can be described for each axis, with the horizontal axis (axis 1) representing the primary environmental gradient and the vertical axis (axis 2) describing a secondary gradient. Species that occur nearer the origin are indicative of (a) species with too few detections to infer habitat associations, (b) habitat generalists, or (c) those that respond to intermediate conditions along the gradients described by the axes. Species that are plotted farther away from the origin can be regarded as correlated with a particular habitat variable or suite of variables. The length of the vector from the origin to the location of the habitat variable in space is indicative of the strength of the correlation between the habitat variable and the gradient described for each axis.

A typical biplot resulting from a COIA in shown in Figure 3-4. In this example, COIA combined information on the relative abundance of amphibians and habitat variables measured along upland habitats of the control and logged treatments ten years after logging. Tailed Frogs (ASTR) were correlated with large Douglas-fir on upland habitats of the control site and their abundance was low and not correlated with any particular habitat features at cut sites. At harvested sites, Western Red-backed Salamanders (PLVE), Ensatina (ENES), or Tailed Frogs were not directly affiliated with the environmental gradients described by axis 1 or 2. The relative abundance of Western Red-backed Salamanders and Ensatina was higher when the upland habitats contained large conifers (i.e., Western Hemlock, *Tsuga heterophylla* and Western Redcedar, *Thuja plicata*) with abundant CWD and increasing rock availability. Tailed Frogs were more abundant when large Douglas-fir persisted in the upland habitats. In this example, the biplots suggest that the relative abundance of Tailed Frogs was negatively affected by logging, that Western Red-backed Salamanders were abundant in upland habitats and associated with coarse woody debris, and that Ensatinas were abundant with more plasticity in terms of habitat selection in unlogged and logged upland habitats.

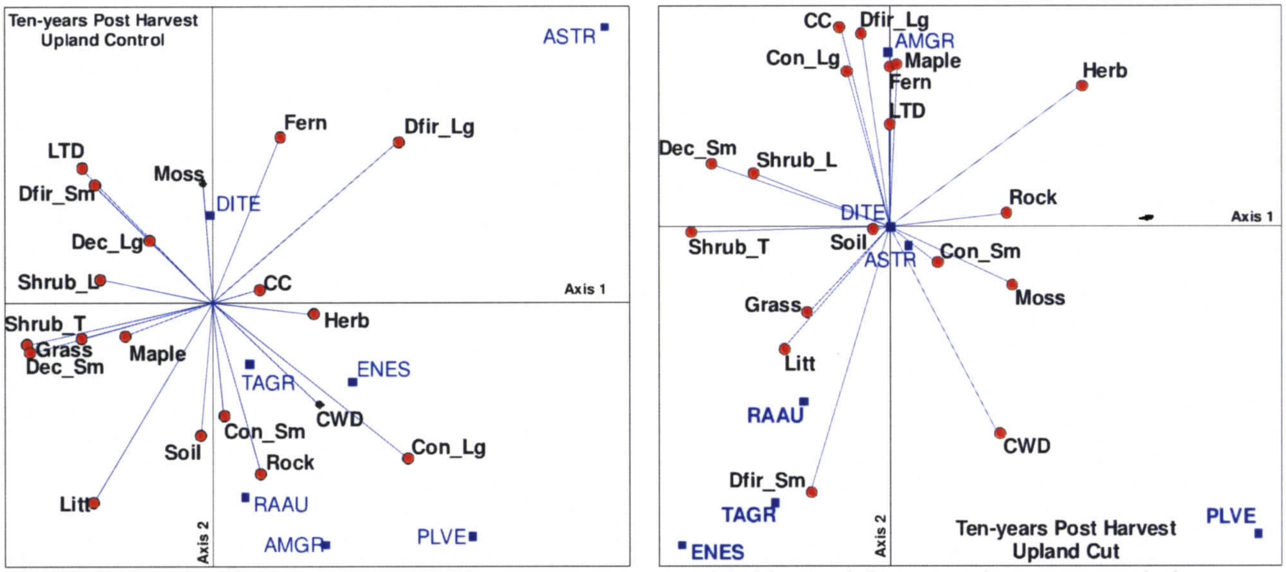


Figure 3-4. Amphibian-habitat relationships in upland habitats of the control treatment relative to logged sites (modified and state) ten years after logging. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = Ambystoma gracile; ASTR = Ascaphus truei; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa*.

Results

Habitat associations were described for both common and widely distributed species of amphibians (Western Red-backed Salamanders, Ensatina, and Tailed frogs) and for species that were less common and more narrowly distributed at my study sites (Pacific Giant Salamanders, Rough-skinned Newts, Northwestern Salamanders, and Red-legged Frogs).

Common, abundant species often are typical of many seral stages (Western Red-backed Salamanders and Ensatina), whereas other species may be relatively common, but apparently restricted to particular seral stages (e.g., Tailed Frogs in older forest dominated by Douglas-fir). In general, forest habitat relationships have not been described for the less common or narrowly distributed species of amphibians that occur in second-growth forests. The COIA provided an opportunity to describe some of the general relationships these species have with habitat attributes measured in a changing landscape.

Riparian and upland forests are functionally and structurally different; therefore, I chose to treat my analyses of habitat relationships separately for each distinct habitat type but comment on how the RMZ may influence the upland forest at harvested sites (and vice versa). Discussion of habitat associations is couched in a temporal context to provide an appreciation of how habitat associations changed over time at the unlogged reference sites and at the buffered sites. As with the discussion of relative abundance (Chapter 2), it was necessary to first establish habitat relationships that existed prior to logging, then to document how those relationships changed across time at the reference sites to obtain a sense of the variation associated with habitat use by each species that was related to forest succession (and not related to logging). Finally, a comparison of the state and modified buffered sites is made with the pre-harvest associations and with the reference treatment to determine if habitat associations changed in riparian buffers or in logged upland habitats.

Only illustrative figures are provided in the Results section; all biplots for each sampling interval, treatment, and transect are provided in Appendix B and Appendix C.

Riparian Habitat Associations

Pre-harvest

The characterization of habitat associations prior to harvest served as a baseline for temporal comparisons of the changes in riparian forests of the reference sites and both buffered treatments. In all three sampling intervals, the riparian forest at the reference sites was characterized by high structural complexity and increasing heterogeneity. The pre-harvest biplot (Figure 3-5) combined relative abundance and habitat attribute data obtained from all 18 sites (i.e., regardless of treatment because treatments had not yet been applied) and revealed a gradient tending towards larger Douglas-fir trees, abundant woody debris and small deciduous and coniferous trees in the understory along axis 1, which was typical of the maturing riparian forests at my study sites. Axis 2 described an environmental gradient tending away from bare soil to a more structurally complex habitat with large coniferous trees (cedar and hemlock) with large deciduous trees (bigleaf maple, *Acer macrophyllum*) comprising a secondary component of the overstory. In this case, axis 2 reflected (to a large degree) the environmental gradient observed on axis 1 and both axes described an environmental gradient of increasing forest age and structural complexity. The majority of the variation in the data was described by axis 1 (65.7%) with an additional 12.6% explained by axis 2.

The relative abundance of the three widely distributed species was strongly associated with these gradients. The abundance of Western Red-backed Salamanders was negatively correlated with axis 1, indicating that this species was more abundant at sites dominated by habitat components typical of younger seral forests, and in general was more abundant when the volume of deciduous canopy cover increased. Ensatinas were correlated negatively with axis 1 and 2 and had an association with large deciduous trees and structural habitat complexity at the shrub level (shrubs ≤ 1.3 m in height). Relative abundance of Tailed Frogs was positively correlated with axis 2 suggesting a strong correlation between increasing relative abundance and increasing forest age and increasing canopy cover (decreasing forest openness).

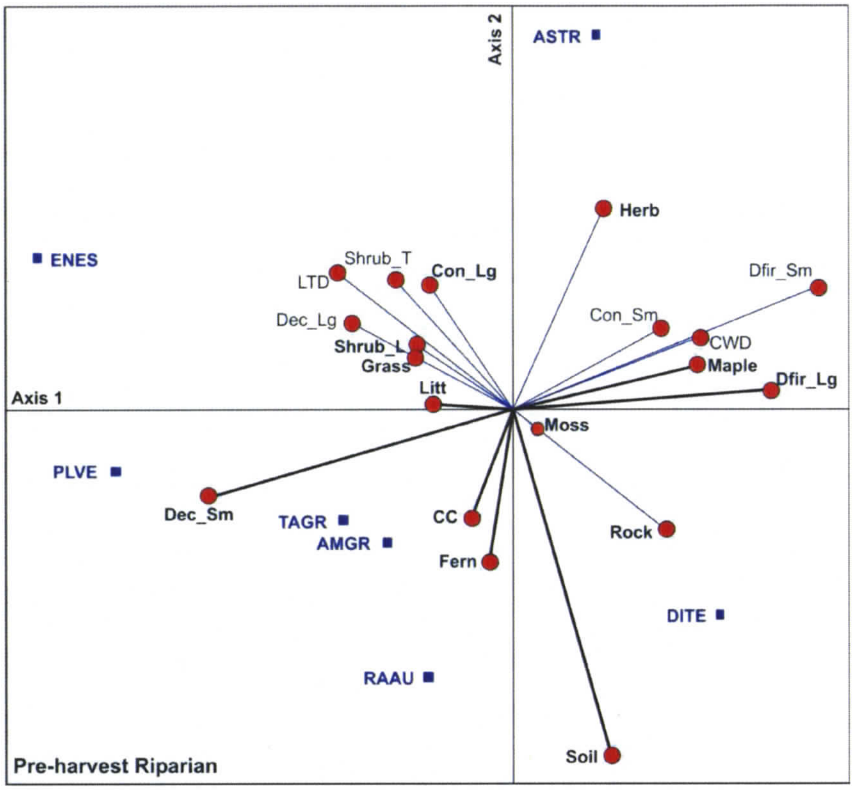


Figure 3-5. Amphibian-habitat relationships in riparian habitats prior to logging. Thick black lines and bold text indicate habitat variables that describe the gradient along each axis. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = *Ambystoma gracile*; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa*.

The relative abundance of Red-legged frogs was associated with increasing canopy cover and decreasing coniferous tree cover and was higher in habitats containing ferns (e.g., *Polystichum munitum* and *Pteridium aquilinum*). Rough-skinned Newts and Northwestern Salamanders were more likely to be abundant in habitats characterized by decreasing forest openness (increasing canopy cover) with fewer large trees. Fern cover appears to have been more important for Northwestern Salamanders than it was for Rough-skinned Newts. Pacific Giant Salamanders were most abundant in habitats with large Douglas-fir trees and rocky soils. Increasing moss and fern cover were also positively associated with the relative abundance of Pacific Giant Salamanders.

Post-Harvest Reference Sites

The variation in habitat associations observed for the common species (Western Red-backed Salamanders, Ensatinas, and Tailed Frogs) at the reference sites was minimal immediately after logging and consistent with the associations described for the pre-harvest period. Ten years following logging, Western Red-backed Salamanders and Ensatinas continued to occupy similar habitats (relative to each other) and the relative abundance of these two species was strongly associated with increasing numbers of large coniferous and deciduous trees and increasing numbers of large Douglas-fir. Ten years after logging, the relative abundance of Tailed Frogs was not correlated with large conifers or Douglas-fir trees. Rather, increasing rock and exposed soil appeared to be more highly correlated with numbers of Tailed Frogs than did the presence of large Douglas-firs (Figure 3-5).

For species not commonly encountered, some interesting patterns were observed in riparian habitats of the reference sites over time. The relative abundance of Northwestern Salamanders was always strongly associated with increasing fern cover in each sampling interval. In the first-post-harvest sampling interval, the relative abundance of Rough-skinned Newts, Red-legged Frogs, and Pacific Giant Salamanders was too low (see Chapter 2) to derive any meaningful habitat relationships. However, in the ten-year post-harvest sampling interval, the relative abundance of all three species was strongly associated with increasing numbers of large coniferous trees, large deciduous trees, and large Douglas-fir, which was consistent with both Western Red-backed Salamanders and Ensatina. The presence of large coniferous and deciduous trees in a heterogeneous, structurally complex forest was positively correlated with increasing relative abundance of terrestrial and semi-aquatic amphibians.

Post-Harvest Buffered Sites

Two years after logging there was no consistency in the habitat associations indicated by the biplots for each of the three treatments for Western Red-backed Salamanders, Ensatinas, or Tailed Frogs. The relative abundance of Tailed Frogs was associated with increasing numbers of large conifers at state buffered sites and with increasing cover of coarse woody debris at modified buffered sites. Although there was a difference in habitat-association between treatments, the relationship between relative abundance and large conifers or coarse woody debris was consistent with the pre-harvest and reference site habitat-associations. Ten years following logging, numbers of Tailed Frogs were correlated with increasing deciduous leaf litter cover and depth and increasing canopy cover, and at both treatments, Tailed Frogs occurred in very low numbers (Chapter 2). At both buffered treatments, numbers of Ensatinas and Northwestern Salamanders were positively correlated with increasing canopy cover and increasing numbers of maple, an association that differed from the habitat associations noted before logging and at the reference sites. These associations persisted into the ten-year post-harvest sampling interval, although the relative abundance of both species was also positively associated with increased volumes of coarse woody debris.

At the modified and state buffered sites, the relative abundance of Western Red-backed Salamanders was associated with small coniferous trees (state) and moss and rock cover (modified) in both the two-year and ten-year post-harvest sampling intervals, representing a departure from the habitat associations described for the pre-harvest period.

The relationship between relative abundance of Red-legged Frogs and habitat attributes was not consistent across time at the buffered sites, nor was relative abundance correlated with a specific habitat attribute, which suggests that Red-legged Frogs are generalists. There was some correlation between the habitat-associations at the state and modified treatments, but the differences observed may be due to habitat variability at the site level and are not necessarily indicative of real habitat differences. Where Red-legged Frogs occur, they are generally abundant and do not appear to be associated with a particular habitat attribute. Rather, it is an overall habitat condition that includes high moisture, access to escape habitat, and increasing levels of shade that dictate where this species occurs.

Rough-skinned Newts were not documented in the two-year post-harvest sampling interval, so habitat associations can not be described. Ten years following logging, the relative abundance of this species was positively associated with increasing numbers of large Douglas-fir and increasing rock cover, a pattern consistent with the associations described for the pre-harvest riparian and for the reference sites in the ten-year post-harvest period.

Upland Habitat Associations

Pre-harvest

The characterization of habitat associations prior to harvest in upland habitats served as a baseline for the comparison of post-harvest habitat associations at the reference sites and the state and modified buffered treatments. Upland habitats in the pre-harvest period were characterized by coniferous tree dominance with a component of large deciduous trees and smaller coniferous trees in the understory. In general, upland habitats were even-aged stands dominated by Douglas-fir with little heterogeneity and low species diversity. Axis 1 of the pre-harvest upland biplot (Figure 3-6) describes a gradient of increasing numbers of large conifers in both the overstory and understory suggesting a maturing and relatively homogeneous second growth upland forest with abundant coarse woody debris (Figure 3-6). Axis 2 describes a gradient of declining deciduous representation in the forest followed by an opening of the forest floor due to increasing canopy cover. Axis 1 explains 62.4% of the total variation in the data and axis 2 explains a further 16.3%.

Under those conditions, Western Red-backed Salamanders were most abundant in upland habitats of increasing forest age with greater volumes of coarse woody debris, and most abundant in habitats characterized by increasing canopy cover, increasing herb growth, and increasing area of exposed soil. Increasing litter depth was also associated with increasing Western Red-backed Salamander abundance. The relative abundance of Ensatina was strongly correlated with axis 2, suggesting that habitats with increasing canopy cover and herbaceous growth supported higher populations of this species; tree species did not appear to be important, but the upland forests were dominated by coniferous trees, primarily Douglas-fir. The upland forests were also characterized by high volumes of coarse woody debris, a habitat attribute known to be positively correlated with the relative abundance of Ensatina. Tailed Frogs occupied a position between the two gradients and were more abundant in habitats dominated by forests of increasing canopy cover, rock cover, and coarse woody debris.

Rough-skinned Newts, Northwestern Salamanders, and Red-legged Frogs were negatively associated with axis 2 suggesting that the relative abundance of these species was correlated with stands dominated by large and small deciduous trees and decreasing canopy cover. Pacific Giant Salamanders were not as abundant on upland transects, but when they were present, they were associated with large conifers, maple, and moss.

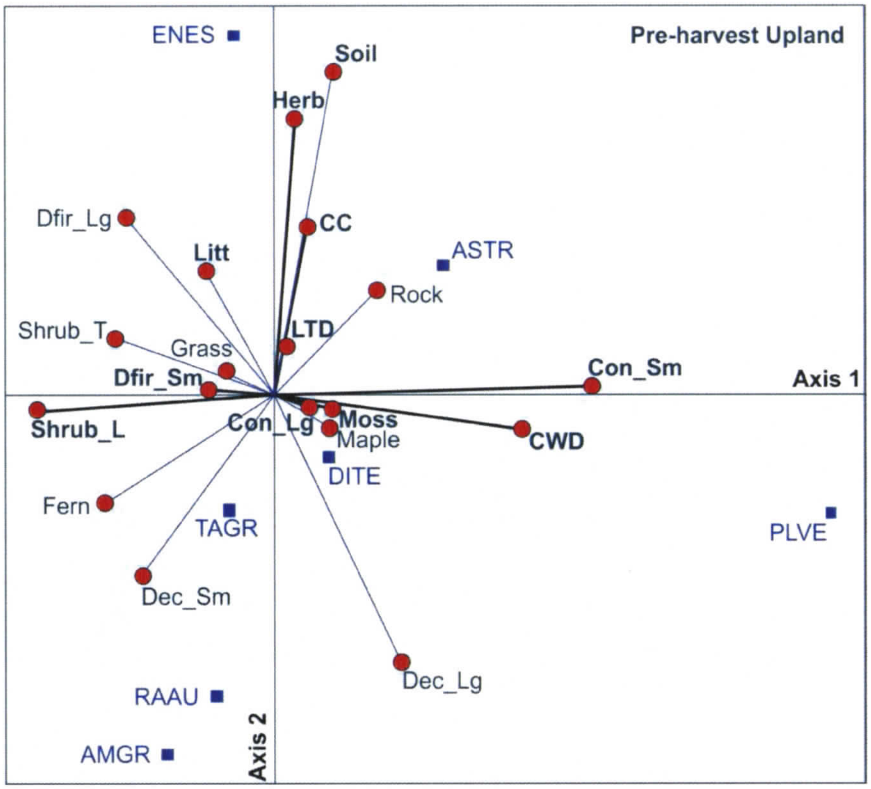


Figure 3-6. Amphibian-habitat relationships in upland habitats prior to logging. Thick black lines and bold text indicate habitat variables that describe the gradient along each axis. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = *Ambystoma gracile*; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa.*

Post-harvest Reference Sites

The upland habitats of the reference sites remained constant over time, with few changes observed. Upland habitats continued to be characterized as homogeneous even-aged forests dominated by Douglas-fir with low species diversity. Two years after logging, the relative abundance of Western Red-backed Salamanders and Ensatina was associated with an increasing number of large conifers, increasing canopy cover, and small conifers in the understory. Tailed Frogs, on the other hand, were more abundant in upland forest dominated by Douglas-fir. These relationships persisted through the ten-year post-harvest sampling interval. The amphibian-habitat associations were most similar in the two- and ten-year post-harvest sampling intervals and both differed slightly from those observed prior to harvest with the difference likely attributable to forest succession. The relative abundance of Red-legged Frogs, Pacific Giant Salamanders, Northwestern Salamanders, and Rough-skinned Newts was loosely associated with the same habitat attributes as Western Red-backed Salamanders and Ensatinas. Ten years following logging, numbers of Pacific Giant Salamanders were closely associated with increasing moss cover, increasing fern cover, increasing litter depth, and increasing numbers of large Douglas-fir trees in the overstory.

Post-Harvest Buffered Sites

The environmental conditions of the upland habitats at logged sites (both types combined) reflected gradients expected immediately after logging. Axis 1 (85.8%) was characterized by few small coniferous trees, increasing herbaceous cover, limited fern cover and a few large Douglas-fir (leave trees) (Figure 3-7). Axis 2 (11.2%) describes an environment of few shrubs, little coarse woody debris, and no large or small deciduous trees. In this case, axis 2 reflects to a large degree the gradient described by axis 1. Under these conditions, the relative abundance of Western Red-backed Salamanders was negatively correlated with axis 1 and was associated with small conifers, rocky substrates, and exposed soil. The relative abundance of Ensatina was correlated with both axis 1 and 2 and appears to be associated with increasing canopy cover and large conifers. Tailed Frogs showed a positive correlation with both axes with some association with large Douglas-firs, although this relationship was weak owing to the paucity of large trees in the uplands of harvested sites. The Red-legged Frog was negatively correlated with axis 2 and its relative abundance was related to the presence of large deciduous trees and maple, which were more prominent in riparian habitats (Figure 3-5). Rough-skinned Newts were more abundant in upland habitats where deciduous litter depth was greater and where rock and litter cover were higher. Given that these conditions were associated with an increase in maple cover, and that the position of Rough-skinned Newts in Figure 3-7 indicates a negative relationship with Axis 2, which was characterized by an increase in maple cover, it follows that this species was not commonly encountered on upland habitats two years following logging. The relative abundance of Northwestern Salamanders and Pacific Giant Salamanders was too low to describe any meaningful habitat associations.

Ten years following logging the upland habitats of the buffered sites had changed considerably with abundant regenerating Douglas-fir, coniferous trees, vine maple, and ferns dominating the landscape (Figure 3-8). These changes were expected given that the upland sites were replanted with Douglas-fir shortly after logging. Vine maple is not a merchantable species and was likely left during logging and ferns can recolonise an area relatively quickly. Other coniferous and deciduous tree species that were present likely grew from seed that originated from adjacent second-growth forests, where those species are abundant. The habitat associations of terrestrial amphibians changed because of the change in seral stage. Higher numbers of Western Red-backed Salamanders were associated with abundant coarse woody debris, higher moss cover, and more small coniferous trees in the ten-year post-harvest sampling interval. The relative abundance of Ensatinas was associated with increasing numbers of small Douglas-fir and increasing deciduous leaf litter depth. Tailed Frog numbers were lower in upland habitats ten years following logging, which is the reason why the position of Tailed Frogs in Figure 3-8 is close to the origin of both axes.

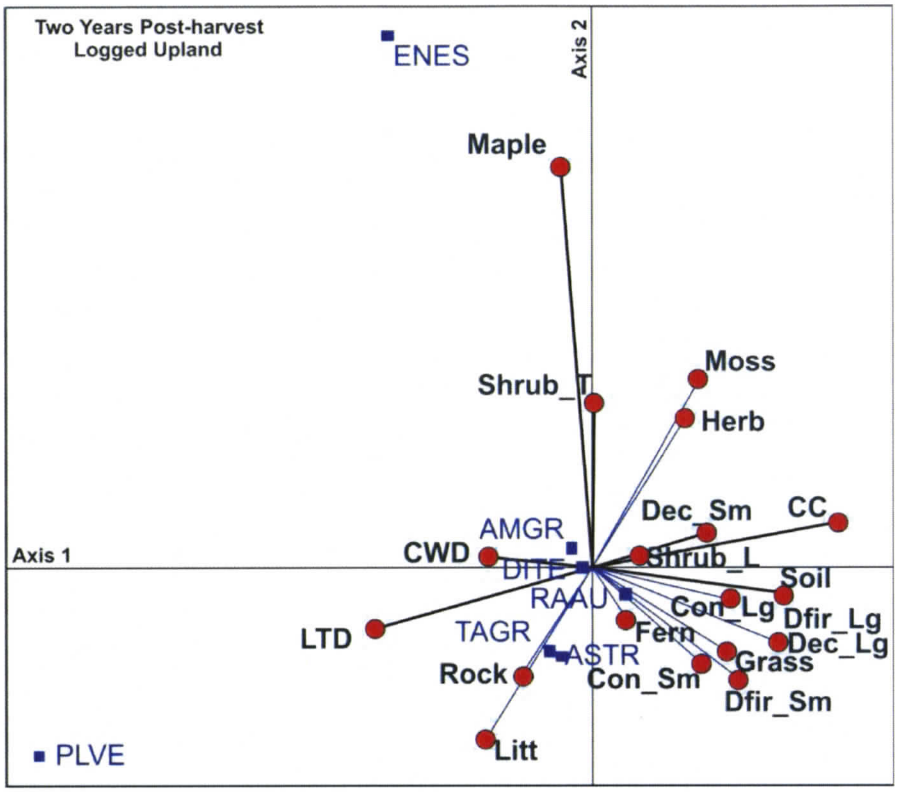


Figure 3-7. Amphibian-habitat relationships in upland habitats two years after logging. Thick black lines and bold text indicate habitat variables that describe the gradient along each axis. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = *Ambystoma gracile*; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa*.

Pacific Giant Salamanders were not documented on upland habitats ten years following logging and their position at the origin of both axes of Figure 3-8 is indicative of their absence. Northwestern Salamanders were positively associated with increasing maple cover, increasing numbers of large Douglas-fir and increasing cover of ferns. Both Red-legged Frogs and Rough-skinned Newts were more abundant when upland habitats had deeper leaf litter and more small Douglas-fir trees.

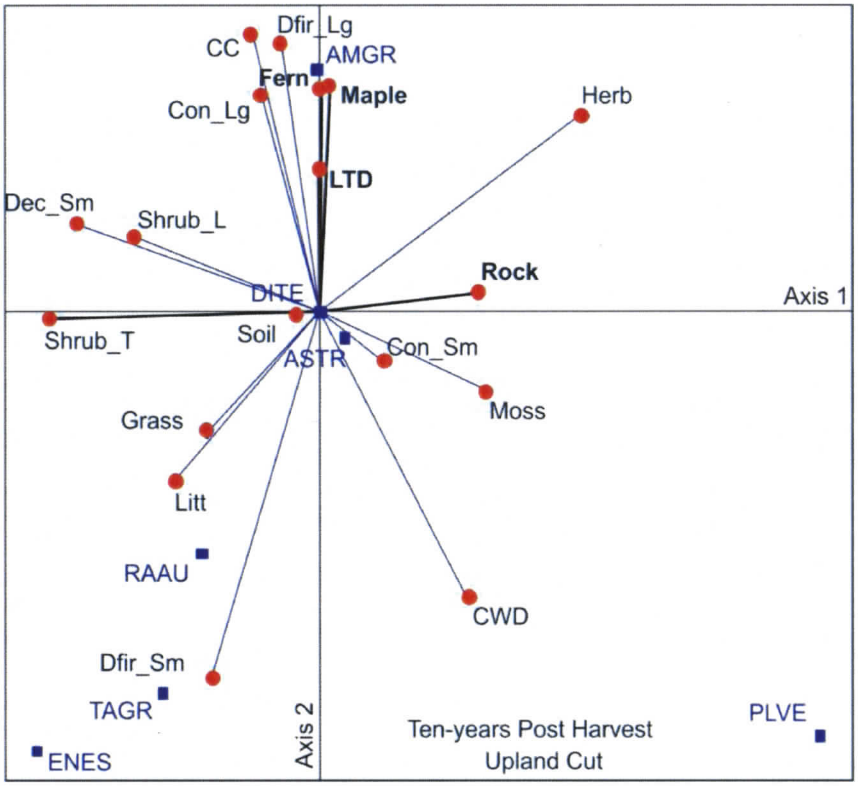


Figure 3-8. Amphibian-habitat relationships in upland habitats ten years after logging. Thick black lines and bold text indicate habitat variables that describe the gradient along each axis. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = Ambystoma gracile; ASTR = Ascaphus truei; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa*.

Habitat Structure: Treatments

In theory, there were to be two distinct riparian treatments to compare to the reference sites; however, this was not the case. By proxy, the assignment of treatment type to a site should have defined buffer width (i.e., state = narrow, uniform; modified = wider, more variable). Plotting the normalized score of the PCA on the habitat attribute table relative to the treatments provides a visual indication that the state and modified buffered sites were not measurably different after logging (Figure 3-9). Prior to logging (blue squares), each treatment occupied somewhat different positions in space. Although all sites within each treatment were selected based on specific criteria (See Chapter 1), the riparian zones within each stand were likely different due to the dynamic nature of riparian forests. Two years after logging, the riparian habitats of both the state and modified buffered treatments diverged from their original pre-treatment positions, but they did not separate relative to each other in space, and both treatments could generally be described by the same suite of habitat variables. The only real differences were that the number of large deciduous trees was greater at the modified buffered treatment and more moss was growing at the state buffered sites. Ten years later, the modified and state treatments diverged from their two-year post-harvest position; however, they occupied a similar position in space relative to each other. If the riparian treatments were distinctly different, the two treatments should have been positioned far apart in space immediately after logging, and over time, although the riparian habitats changed, the separation in space should have continued to be apparent and measurable, with some degree of convergence due to the growing of adjacent upland forest. While some of the habitat attributes varied relative to treatment and transect, the vegetation structure and complexity of treatments was not great enough to measure differences between the two treatment types.

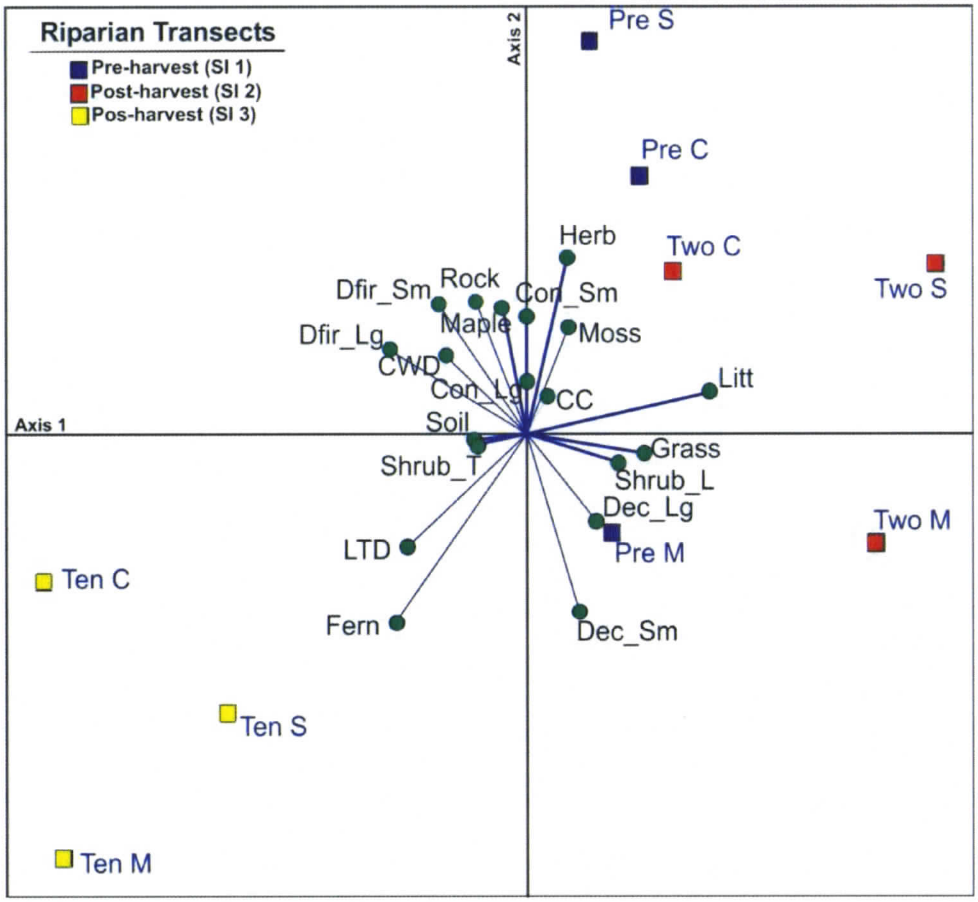


Figure 3-9. Biplot of riparian transect habitat condition by treatment and time interval. The data in this figure represent the mean condition as derived from the normalized score of the PCA on the habitat data matrix. Thick lines denote variables that describe the gradients along each axis. SI 1 = 1992-93; SI 2 = 1995-96; SI 3 = 2003-04; C = Control; M = Modified; S = State. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m.

The riparian habitats of the reference sites varied across time and in association with both the modified and state buffered treatments. Because the reference sites continued to occupy a position in space similar to the buffered sites, with respect to the habitat attributes measured, comparisons of relative abundance made among treatments was justified. Comparisons of the habitat associations of terrestrial salamanders among treatments were also validated.

Examination of habitat conditions for the upland transects of each treatment type shows that the pre-harvest conditions of the modified and state buffered sites were similar to the reference sites and that the reference sites remained relatively constant across time (Figure 3-10). Clustering of the modified and state buffered sites in both post-treatment intervals provides evidence that the logging prescriptions produced ecologically similar results with regard to habitat structure in upland logged habitats over time. This was expected considering that forest harvest prescriptions along upland transects were essentially the same at modified and state buffered sites. Immediately after harvesting, the upland transects were largely devoid of vegetation. By approximately ten years later, modified and state buffered sites showed clear signs of succession, supporting an increased abundance of Douglas-fir, deciduous trees, and berry-producing shrubs (Figure 3-10). As expected, differences at the reference sites were not as large as at logged sites.

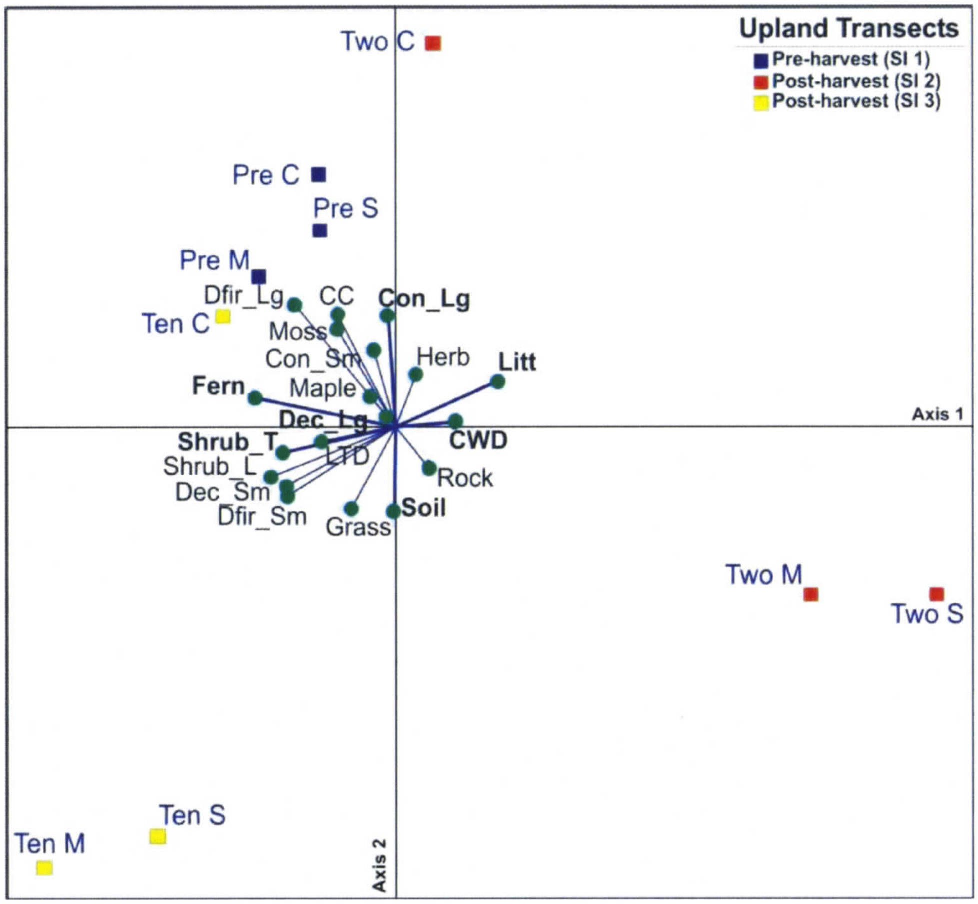


Figure 3-10. Biplot of upland transect habitat condition by treatment and time interval. The data in this figure represent the mean condition as derived from the normalized score of the PCA on the habitat data matrix. Thick lines denote variables that describe the gradients along each axis. SI 1 = 1992-93; SI 2 = 1995-96; SI 3 = 2003-04; C = Control; M = Modified; S = State. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m.

Discussion

Despite continuing forest succession in riparian habitats and major changes in the upland forests, the habitat associations of terrestrial amphibians remained surprisingly consistent over time. Co-inertia analysis revealed that most species of terrestrial amphibians are habitat generalists that are capable of adapting to significant habitat changes. Moreover, most species appeared to be able to seek out specific habitat attributes that provided suitable cover and protection, enabling them to persist on the landscape. Other species, such as Tailed Frogs, were consistently associated with specific features of the landscape, indicating a higher degree of habitat specification.

Co-inertia analysis may be an especially suitable statistical tool to use in studies of landscape ecology because of its flexibility and relative lack of constraints compared to other methods. However, because COIA has not been used to describe habitat associations for amphibians, it was necessary to use the published literature to assess the utility of COIA in describing habitat relationships of amphibians in the Pacific Northwest. Although the published literature on habitat relationships is based on different statistical techniques (e.g., CCA, RDA, multiple regressions), the habitat associations identified for terrestrial amphibians at my study sites were consistent with the literature.

For example, the relative abundance of Western Red-backed Salamanders was positively correlated with habitat attributes of a younger seral forest in all three sampling intervals. Vegetation diversity and cover, used to infer productivity and moisture regime of riparian habitats relative to upland forest, was important because populations of this species are often associated with rocky seeps, springs, and small streams in the northern Puget Trough and Cascade Range foothills in Washington (Leonard 1996; Petranka, 1998). After logging, Western Red-backed Salamanders were associated with deciduous leaf litter, perhaps because deciduous leaf letter provided suitable thermal habitat, security cover, and foraging habitat. This perceived change in habitat association may be indicative of this species' ability to adapt to a changing landscape. Logging in the adjacent upland likely impacted the riparian habitats, but the degree of impact was not measured. Despite the perceived changes in habitat-associations, the relative abundance of Western Red-backed Salamanders was not affected (Chapter 2), which suggests that habitat use by this species is variable, but confined to certain habitat features, namely moss, ferns, coarse woody debris, rocky slopes, and deciduous leaf litter.

Tailed Frogs were consistently associated with large coniferous trees (Western Redcedar, Western hemlock, and Douglas-fir), increasing canopy cover, and increasing coarse woody debris cover. Thus, this species appears associated with components of maturing forests, a notion that is corroborated by the literature (Dupuis et al. 1995; Dupuis and Waterhouse 2001). Pacific Giant Salamanders were common but not abundant in riparian habitats, making it difficult to derive specific habitat correlates. However, this species was always captured in riparian habitats with relatively high canopy cover and abundant cover vegetation such as ferns.

Other species present in riparian habitats did not show a consistent correlation with any particular habitat attributes. However, because their relative abundance did not change over time (see chapter 2), it is apparent that the riparian habitat structure and complexity retained at the state and modified buffered treatments was sufficient to enable amphibians to persist at densities comparable to pre-harvest levels.

The riparian habitats in each of the treatments contained habitat components and heterogeneity that were suitable for the persistence of both abundance and diversity of amphibians. However, because the state and modified buffered treatments were not measurably different, it is not possible to comment on the effective width of a riparian management zone required to maintain terrestrial amphibian diversity and abundance. Given that the width of the riparian buffer averaged 14 m (state) and 30 m (modified) a buffer width within that range is sufficient to preserve habitat characteristics required to maintain species' relative abundance up to 10 years after logging. However, these values should be used as minimum widths because edge effects can be more pronounced when buffers are narrower (deMaynadier and Hunter 1998; Karraker and Welsh 2006). To ensure that species like Western Red-backed Salamanders, Tailed Frogs, and Pacific Giant Salamanders persist in riparian management zones, it is imperative that these zones be large enough to be protected from wind events that could lead to extensive blowdown in the riparian zone. Further, the habitat structure of the riparian zone should not be compromised by thinning, or other silvicultural activities that could degrade the suitability of the riparian management zone for amphibians.

Plethodontid salamander (Western Red-backed and Ensatina) populations survived the large-scale habitat perturbation associated with clearcut logging in upland habitats and populations of both of these species were not adversely affected as evidenced by the lack of significant changes in relative abundance attributable to treatment effects (chapter 2). The habitat associations of both of these species necessarily changed before and after logging because of the removal of the overstory and serious modification of the soil through compaction and scraping and changes in forest floor cover related to the removal of coarse woody debris, ferns, shrubs, and small trees. During periods of extreme environmental conditions, such as surface freezing or high temperatures, plethodontid salamanders will go underground and take refuge in small mammal burrows or natural crevices in the soil or talus (Stebbins, 1954; Dumas 1956; Ovaska and Gregory 1989; Petranka 1998). It is conceivable that both Western Red-backed and Ensatina salamanders retreat to underground burrows during periods of large-scale habitat perturbations such as upland logging.

Unlike many Pacific Northwest plethodontid salamanders, Ensatina salamanders tend to be more abundant away from streams (McComb et al. 1993), which is supported by data from this study. In upland habitats, Ensatina abundance was correlated with increasing canopy cover, large coniferous trees, and vine maple, suggesting that this species is associated with a variety of upland habitat attributes provided there is sufficient moisture. However, Ensatina were not strongly correlated with coarse woody debris as has been found in other studies (Bury and Corn 1988). Western Red-backed Salamanders occupied similar habitats in upland forest and their abundance was correlated with increasing cover of coarse woody debris. This helps explain why Western Red-backed Salamander populations were not affected by logging: clearcut sites typically have an abundance of coarse woody debris in the form of downed logs of small diameter or non-merchantable timber. Additionally, although much of the coarse woody debris is piled and burned, there is an abundance of woody material left on the ground after logging, which likely provides suitable security and thermal habitat for Western Red-backed Salamanders.

Some species were noticeably absent from upland habitats (chapter 2) and their absence can be readily explained through an assessment of their habitat relationships in upland forest prior to logging. Before logging the relative abundance of Tailed Frogs was positively correlated with increasing canopy cover. After logging, the canopy cover was effectively zero, as was the abundance of Tailed Frogs. Relative abundance of Pacific Giant Salamanders was correlated with increasing numbers of large coniferous and deciduous trees in the overstory. After logging, both of these habitat components were removed, which likely affected the movement of Pacific Giant Salamanders, restricting them to riparian habitats (Johnston and Frid 2002). Grialou et al. (2000) found that Pacific Giant Salamanders were absent from sites two years after clearcutting.

To assess the utility of a management strategy that includes habitat retention for the maintenance of biodiversity, it is necessary to describe the habitat associations for focal species prior to treatment application and to monitor how habitat associations vary across time. Although COIA continues to be an under-used multivariate technique, it has been used recently to describe species-habitat associations (e.g., Diallo et al. 2006; Sirami et al. 2007). The utility of a COIA was evident in my study as it provided an efficient way to visualize and describe the habitat associations of many species of terrestrial amphibians before and after logging and to compare the habitat attributes in riparian and upland habitats of two buffered treatments.

Forest managers require direction from ecologists to manage for biodiversity on landscapes managed for timber. This requires that ecological studies occur at broader scales so that region-wide patterns of diversity, relative abundance, and habitat associations can be detected. With an increase in scale comes an increase in cost and time required to complete the study. As a trade-off, ecologists are faced with reducing the number of sites and treatments, or reducing the geographic scale of the study. If region-wide biodiversity management is the premise for a study, then a reduction in replication or treatments is often the only way to make the study economically viable. Under these conditions, attempting to define species-habitat associations using common and widely reported methods of ordination would be erroneous because a major assumption of those techniques would be violated: the number of samples relative to the number of environmental variables would be too low. The introduction of COIA to ecologists by Dolédec and Chessel (1994) provided a viable, robust method with which to describe habitat relationships at a broader scale that is not constrained by the need for large sample sizes. As broader-scale studies are undertaken to establish better biodiversity management plans that include species habitat relationships, co-inertia analysis will likely increase in use because of its adaptability, ease of interpretation, and ability to properly describe habitat relationships.

Chapter 4 Conclusions and Management Implications

Conclusions

My study was the first longer-term study utilizing a BACI design to evaluate the efficacy of riparian management zones in providing habitat for wildlife. My results showed that the variability in response to upland clearcut logging by amphibians makes it difficult to define management strategies that are effective for all species present. In general, the relative abundance, richness, community similarity, and habitat-associations of amphibians did not change because of timber harvest or the retention of riparian management zones around third and fourth order streams in western Washington. This was not a global response, however, as the relative abundance of Pacific Giant Salamanders was not maintained in the riparian habitats of the state buffered treatments and both Pacific Giant Salamanders and Tailed Frogs declined in numbers on upland habitats of both the modified and state buffered sites. Most changes in relative abundance were not attributable to logging, but instead were explained by local or regional population changes.

The COIA provided an indication of species-habitat associations over time and there does not appear to be any component of the environment that was missing at state buffered sites to influence the decline of Pacific Giant Salamanders. The more likely reason for Pacific Giant Salamander decline is related to the reduced area within the riparian buffer zone that forced Pacific Giant Salamanders to seek out larger stands of maturing forests so that they could occupy large enough areas to fulfill their life requisites. From a management perspective, this suggests that a riparian buffer width of at least 30 m is required to maintain the relative abundance and richness of all amphibians in western Washington, at least where Pacific Giant Salamanders are present.

The reason for the decline in numbers of Tailed Frogs in upland habitats of the state and modified buffered sites was evident through the COIA. Two and ten years after logging there were no large Douglas-fir trees in the upland. The habitat-associations described for Tailed Frogs for the pre-harvest sampling interval and at the reference sites over time suggest that this species requires habitat characteristics associated with maturing coniferous forests dominated by Douglas-fir. When these conditions are not met, the habitat suitability, along with the number of Tailed Frogs, declines. Presumably, Tailed Frogs move to adjacent maturing stands of coniferous forest; however, a study comparing the relative abundance of Tailed Frogs in upland clearcuts relative to adjacent stands of maturing timber is required to test this hypothesis.

Management Implications

Extensive forestry management in the Pacific Northwest has historically included clearcutting, prescribed fire, regeneration by seed trees, protection from forest fires, and salvage of timber killed by windthrow or disease (Carey and Harrington 2001). In the last 20 years, planting of Douglas-fir has increased, with most forest stands > 40 years old originating from seed. Current management practices include the retention of seed trees and coarse woody debris and the planting of seedlings. Implicit in the shift to ecosystem management has been the retention of riparian management zones around perennial fish- and non-fish bearing streams, which have been required in some form since 1978.

During the past 10–15 years, increased attention has focused on defining and delineating riparian areas. McComb et al. (1993) reported that a buffer width of 50 m adjacent to second and third order streams in Oregon provides marginal habitat for amphibians and buffers should be > 50 m wide to provide linkages between mature forests. Vesely and McComb (2002) suggested buffers ranging from 43 to 47 m wide would support species richness of amphibians at levels similar to unlogged sites. Recently, Crawford and

Semlitsch (2007) found that a buffer width of 27 m would allow 95% of all species of salamanders at a site to persist and that an additional 50 m should ameliorate edge effects. They recommended that a total buffer of 92.6 m be used in southern Appalachian streams to enable salamander biodiversity to persist. I found that a minimum buffer width of 30 m around third and fourth order streams in western Washington maintained species richness and relative abundance values of terrestrial amphibians at levels similar to those recorded prior to logging.

The minimum width of a riparian management zone continues to be a geographic issue related to the implementation of region-wide management plans that are too general to account for local variability in species richness and diversity. The research on the benefits of riparian management zones is clear (deMaynadier and Hunter 1995; Vesly and McComb 2002; Cushman 2006) and most jurisdictions in Canada and the United Sates require the retention of riparian forest adjacent to upland logged habitats (Lee et al. 2004). The problem faced by land managers is that, far too often, management plans become specific to one group of organisms and do not use biodiversity preservation as the basis for management. For example, the establishment of a 30 m wide buffer to maintain the species richness and relative abundance of terrestrial amphibians may not be suitable for all wildlife groups. The development of a riparian habitat management strategy needs to include provisions for the maintenance of populations of other species on landscapes managed for timber (e.g., ungulates, raptors, and furbearers).

Although riparian management zones retain structural heterogeneity and complexity, the production of homogeneous, simplified even-aged stands of second-growth Douglas-fir forests in upland habitats may, over the long term, lead to localized extirpations of species like the Pacific Giant Salamander. Therefore, it is important to consider not only the geographic relationship to riparian management, which will provide an indication of species richness and abundance, but also to consider the frequency of upland rotation and the type of prescription applied to the upland forest. For example, Perkins and Hunter (2006) recommended that riparian management be a two-tiered approach with no-cut zones in the riparian forest and a partial-cut zone in the adjacent upland. This approach should protect the riparian forest from blowdown and minimize edge effects (deMayandier and Hunter 1998).

For species that decline in abundance because of logging, management strategies to mitigate those declines have been proposed. Carey and Harrington (2001) concluded that management-induced homogeneity and simplification (i.e., reduction of complexity) posed a real danger that small mammal communities would not be able to support predator populations. They proposed that active management for habitat complexity on long rotations (> 90 years) may be necessary to conserve the diversity attributed to maturing forests. Because terrestrial amphibian communities are inherently linked to many forest ecosystem processes, the development of biodiversity management strategies must be considered at a broader scale and should not be based on single-species conservation. The introduction of heterogeneity into homogeneous, even-aged stands has been shown to have positive effects on biodiversity and ecosystem function in the short term (< 5 years) (Carey 2003); longer-term studies are required to determine if the positive effects are long-lasting.

Since this study's inception in 1991, there have been changes to the Washington Forest Practices that have implications for my findings. The Forest Practice Rules of 1988 required a riparian buffer that met the state configuration (i.e., not less than 7.5 m from the ordinary high water mark) for both fish-bearing (Type 3) and non-fish bearing (type 4) perennial streams. The development of the modified riparian prescription was an alternative to the state buffer that provided for greater structural complexity, heterogeneity, and ultimately greater diversity for both flora and fauna. Lee et al. (2004) identified the current trend in riparian management prescriptions as tending towards site-specific buffers that vary amongst broadly similar harvest areas (e.g. landscape unit) to within a single harvest area (e.g., watershed). The Washington State Forest Practice Rules of 2001 seem to fit this model, as they are site-specific with many options. Lee et al. (2004) suggest that the primary benefit of this type of prescription is the identification of well-defined criteria to delineate the riparian zone. These criteria are specifically defined by the modifying factors selected by jurisdictions, and buffers are applied in a predictable response to these criteria.

The caveat to tailor-made buffers is the greater complexity in guidelines. For example, Washington now describes three zones of management for Type F streams (Type 3): the core, inner, and outer zones, with various levels of tree removal, thinning, hardwood conversion, and other activities permitted within these zones depending on the site class of land, the management harvest option, and the bankfull width of the stream. In general, the site class will form the RMZ prescription. It appears that riparian management in western Washington has become (necessarily) site specific. This implies that applying a one-size-fits-all approach to riparian management has been set aside in favour of a more intensive, site-specific approach, which is consistent with Lee et al. (2004). For Type Np streams, or perennial non-fish-bearing streams (= Type 4), the riparian management zone rules are slightly less complicated; however, there is ample room for site-specific management. Considering that the riparian management zone rules have evolved to embrace a site-specific approach, it seems only fitting that forest management in general adopt the same principles when considering biodiversity. Managing for biodiversity on a regional scale does not account for variation at the landscape or site level within the region, which could have dire consequences for species that are limited geographically, that occur at naturally low densities, or that are particularly sensitive to habitat change. As an alternative to the status quo, management that focuses on stand heterogeneity (as opposed to tree species monocultures with reduced diversity) should produce landscapes with high biocomplexity and biodiversity at multiple scales; therefore, these landscapes should be resilient in the face of disturbance (Holling 2001).

Several factors potentially influence the veracity of my study's results or limit the extent to which the conclusions can be used to aid in the management and conservation of terrestrial amphibians in coniferous forests of the Pacific Northwest. Many of those factors were unmeasured and are presented to promote thought and aid in the development of future studies on the interactions between amphibians and habitats in managed landscapes.

First, if the relative abundance of amphibians at harvested sites is overestimated, the severity of the harvest on the amphibian population is underestimated and, conversely, underestimating the relative abundance of amphibians at treated sites results in overestimation of the severity of the harvest (Knapp 1999). Several factors can influence the surface activity of amphibians, including temperature, precipitation (Gibbons and Bennett, 1974; Ascaphus Consulting 2006; Johnston and Frid 2002), elevation, population size (Hairston 1980, 1986), and food availability (Mitchell et al. 1996). Of these factors, the relationship between food availability and upland timber harvest has not been researched in the Pacific Northwest.

Second, accurate comparisons of species richness values among treatments and transects requires that all species potentially present at a site be documented to avoid falsely labelling a species as not-present. This requires the use of various methods of species detections and sampling that spans more than one season. The sampling used in this study was not suited to the detection of all species potentially present at each site and was restricted to the fall season. Expanding the sampling period to include the spring and including other sampling techniques would undoubtedly increase the species richness values recorded during this study.

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Appendices

Appendix A. Ecological description of each site sampled in western Washington, 1992 – 2004. Refer to Figure 1-1 for distribution of study sites. -- data not available.

				Elevation (m ASL)		Stream Gradient	Stand Age[1]							
Site Name	Treatment	County	Physiographic Province[2]	Min	Max	(%)	Yr 1	Yr 14	Dominant Tree	Stream Type	Bankfull Width (m)	Shape	Riparian CC (%)[3]	Lithology[4]
Abernathy	Control	Cowlitz	OP/SW	362	431	16	55-65	68-78	Douglas-fir	Type 3	5.0	Sloping	71	Basalt flows
Elbe Hills	Control	Pierce	WSC	554	609	10	55-65	68-78	Douglas-fir	Type 3	3.2	V-shaped	91	Volcanclastic deposits or rocks
Hotel Creek	Control	King	PT	277	303	4	55-65	68-78	Douglas-fir	Type 3	2.4	V-shaped	99	Continetal glacial outwash - Fraser Age
Porter Creek	Control	Thurston	PT	285	290	3	55-65	68-78	Douglas-fir	Type 3	5.9	V-shaped	95	Basalt flows and flow breccias
Taylor Creek	Control	King	PT	415	424	2	55-65	68-78	Douglas-fir	Type 3	6.5	V-shaped	94	Continental glacial till - Fraser Age
Vail	Control	Lewis	PT	--	--	--	55-65	68-78	Douglas-fir	Type 3	--	--	--	Andesite Flows
West Fork Falls Creek	Control	Thurston	PT	379	463	20	55-65	68-78	Douglas-fir	Type 3	3.26	V-shaped	92	Basalt flows and flow breccias
Bluetick	Modified	Grays Harbor	PT	110	151	7	55-65	68-78	Douglas-fir	Type 3	2.0	Undercut	94	Marine sedimentary rocks
Eleven 31	Modified	Lewis	PT	493	561	6	55-65	68-78	Douglas-fir	Type 3	3.3	V-shaped	93	Andesite flows
Griffen Creek	Modified	King	WSC	157	188	5	55-65	68-78	Douglas-fir	Type 3	4.1	V-shaped	93	Continetal glacial till - Fraser Age
Ms. Black	Modified	Thurston	PT	67	92	3	55-65	68-78	Douglas-fir	Type 3	1.8	Undercut	83	Basalt flows and flow breccias

				Elevation (m ASL)		Stream Gradient (%)	Stand Age[1]							
Site Name	Treatment	County	Physiographic Province[2]	Min	Max		Yr 1	Yr 14	Dominant Tree	Stream Type	Bankfull Width (m)	Shape	Riparian CC (%)[3]	Lithology[4]
Ryderwood 860	Modified	Cowlitz	OP/SW	303	337	8	55-65	68-78	Douglas-fir	Type 3		V-shaped	75	Nearshore sedimentary rocks
Side Rod	Modified	Pierce	WSC	520	548	6	55-65	68-78	Douglas-fir	Type 3	2.7	V-shaped	90	Volcanoclastic deposits or rocks
Eleven 32	State	Lewis	PT	415	501	10	55-65	68-78	Douglas-fir	Type 3	1.3	V-shaped	98	Andesite flows
Kapowsin	State	Pierce	WSC	443	450	2	55-65	68-78	Douglas-fir	Type 3	3.1	V-shaped	51	Basaltic andesite flows
Night Dancer	State	Grays Harbor	PT	125	201	11	55-65	68-78	Douglas-fir	Type 3	1.4	V-shaped	96	Marine sedimentary rocks
Potpourri	State	Thurston	PT	239	249	7	55-65	68-78	Douglas-fir	Type 3	5.2	V-shaped	74	Basalt flows and flow breccias
Ryderwood 1557	State	Cowlitz	OP/SW	333	376	7	55-65	68-78	Douglas-fir	Type 3	3.3	V-shaped	77	Nearshore sedimentary rocks
Simmons Creek	State	Lewis	WSC	422	471	8	55-65	68-78	Douglas-fir	Type 3	3.2	V-shaped	80	Basaltic andesite flows

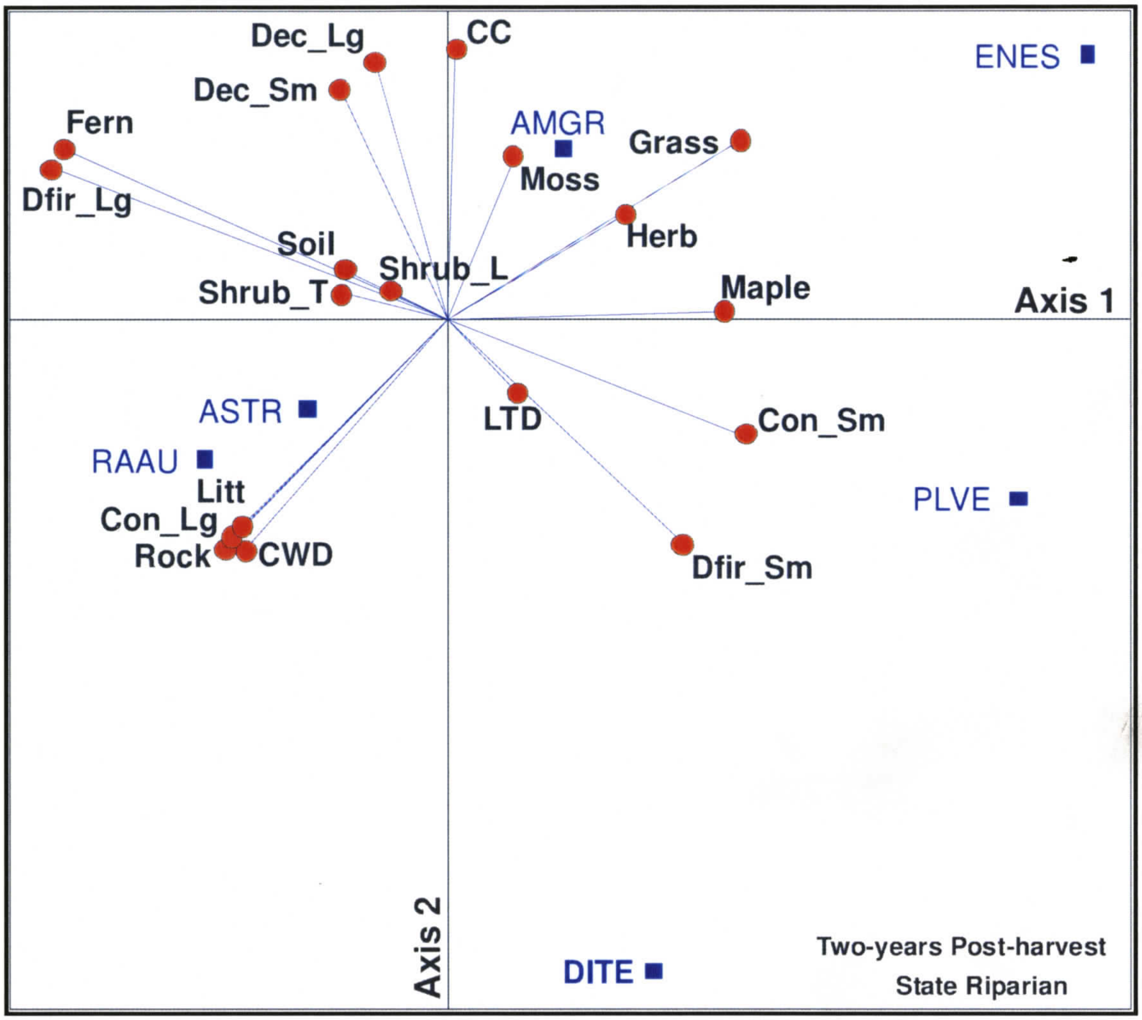
1 Stand Age in years represents estimated stand age at start of study (Year 1 = 1991). Year 14 represents estimated stand age in the last year of field sampling (2004).

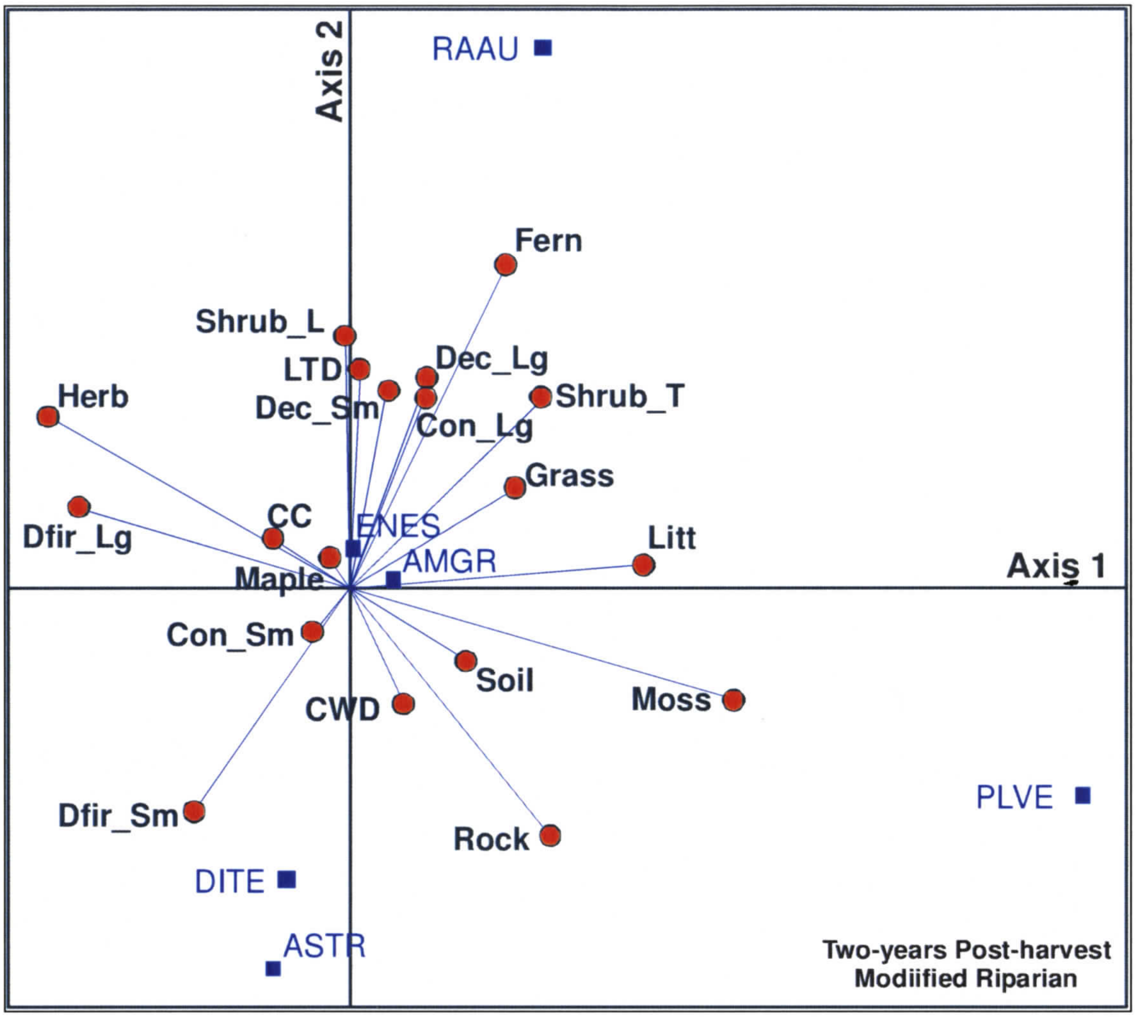
2 OP/SW = Olympic Peninsula and SW Washington; PT = Puget Trough; WSC = Western Slopes and Crest, Washington Cascades Physiographic Provinces

3 Riparian CC (%) is the average canopy cover in the riparian zone measured in 2004.

4 Lithology obtained from http://wa_geology.home.comcast.net/

Appendix B. Amphibian-habitat relationships in riparian habitats two years after logging. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = *Ambystoma gracile*; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa*.




Axis 2
RAAU
Fern
Shrub_L
LTD
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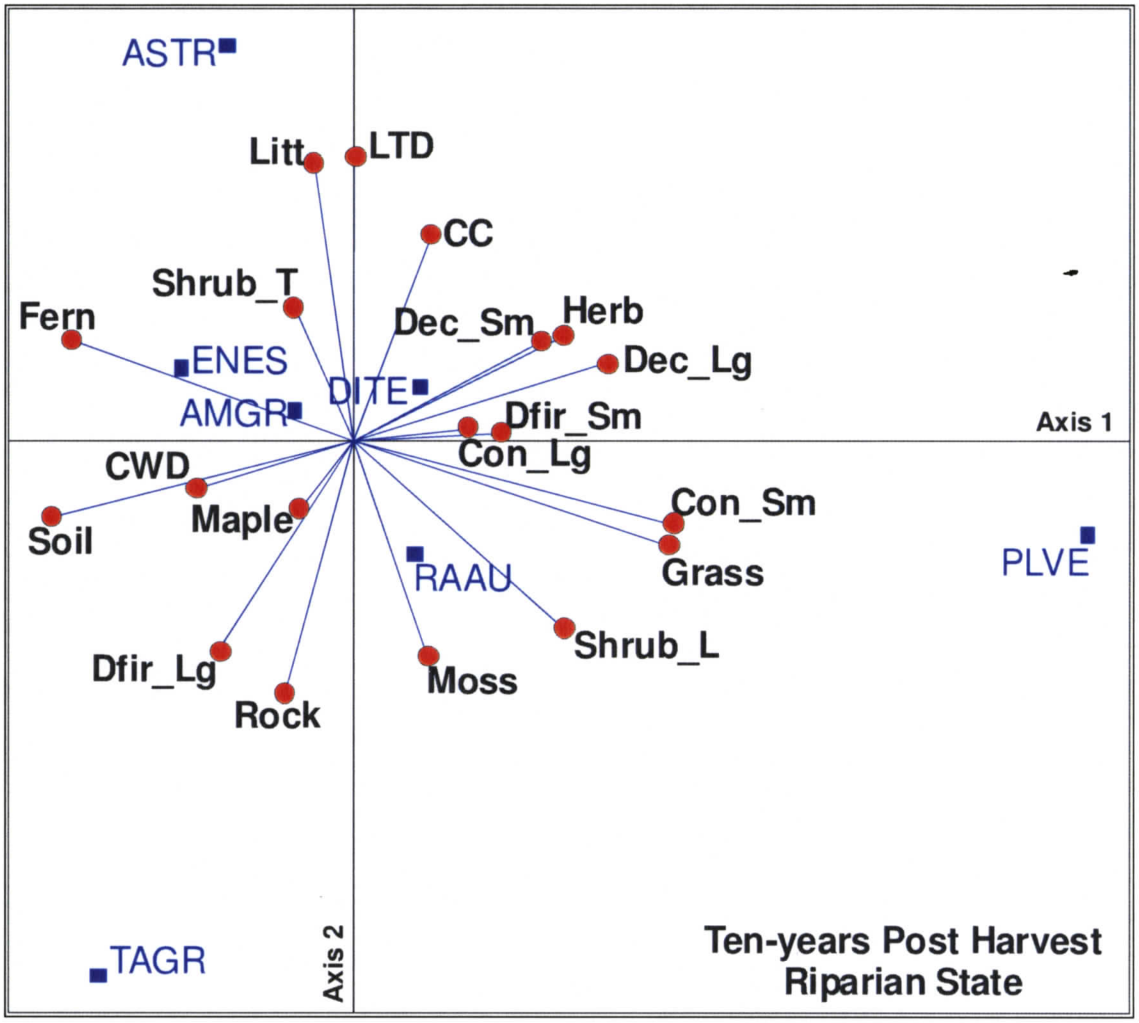
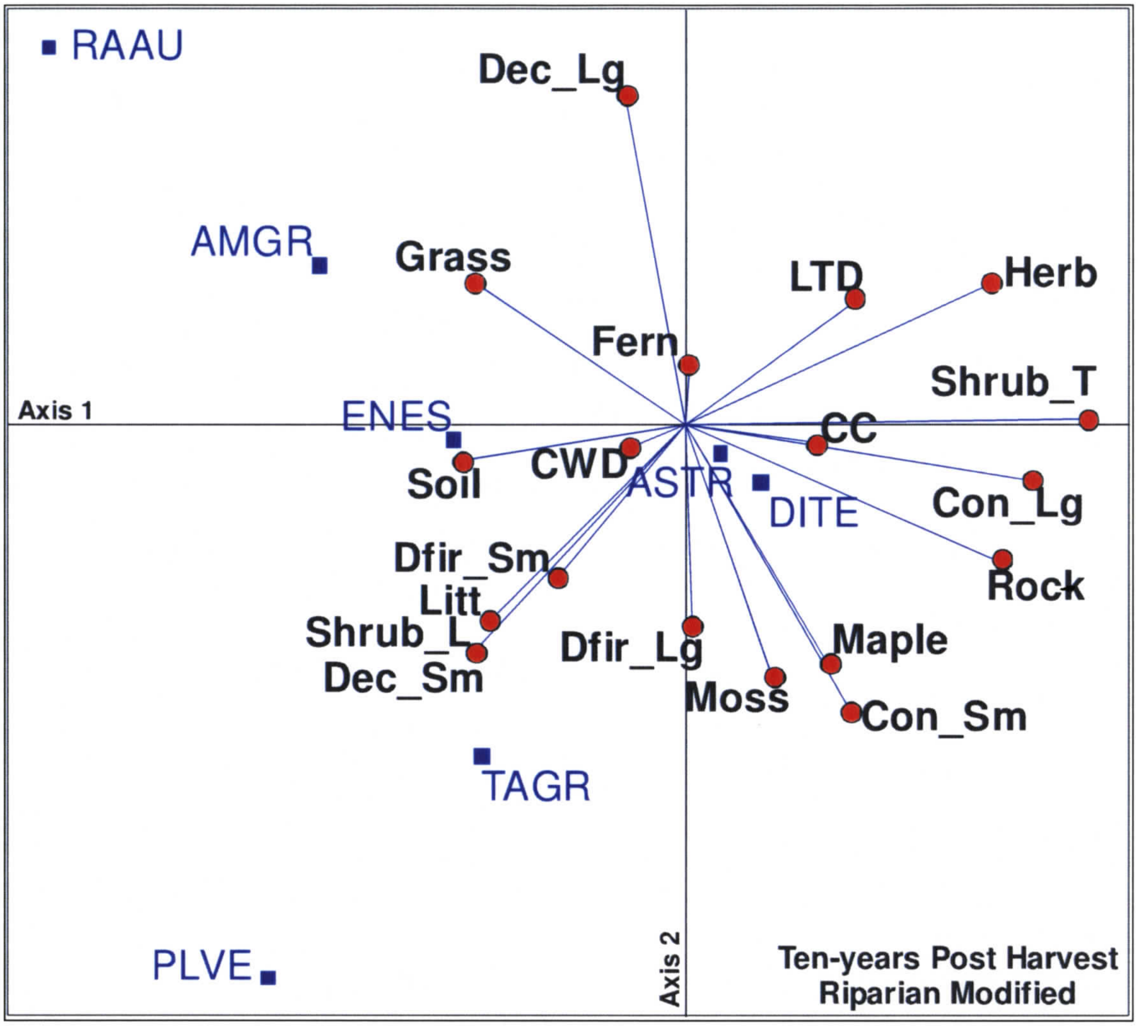
Herb
Dec_Sm
Shrub_T
Con_Lg
Grass
CC
ENES
Dfir_Lg
Litt
AMGR
Maple
Axis 1
Con_Sm
Soil
CWD
Moss
PLVE
Dfir_Sm
Rock
DITE
ASTR
Two-years Post-harvest
Modiified Riparian

Appendix C. Amphibian-habitat relationships in riparian habitats ten years after logging. Shrub_T = tall shrubs; Shrub_L = low shrubs; CC = overstory canopy cover; CWD = coarse woody debris; Fern = fern cover; Grass = grass cover; Herb = herbaceous cover; Litt = deciduous leaf litter cover; LTD = deciduous leaf litter depth; Moss = moss cover; Rock = rock cover; Soil = exposed soil; Maple = vine maple; Dec_Sm = bigleaf maple and red alder < 1/3 m; Dec_Lg = bigleaf maple and red alder > 1.3 m; Con_Sm = western redcedar and western hemlock < 1.3 m; Con_Lg = western redcedar and western hemlock > 1.3 m; Dfir_Sm = Douglas-fir < 1.3 m; Dfir_Lg = Douglas-fir > 1.3 m. AMGR = *Ambystoma gracile*; ASTR = *Ascaphus truei*; DITE = *Dicamptodon tenebrosus*; ENES = *Ensatina eschscholtzii*; PLVE = *P. vehiculum*; RAAU = *Rana aurora*; TAGR = *Taricha granulosa*.




RAAU
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Axis 2
Ten-years Post Harvest
Riparian Modified