

**WOODLAND AMPHIBIAN DISTRIBUTION IN PARKS AND GREENSPACES
OF THE PORTLAND, OREGON METROPOLITAN AREA:
A MULTIPLE SCALE INVESTIGATION**

by

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A thesis submitted in partial fulfillment of the
requirements for the degree of

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ABSTRACT

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Title: Woodland Amphibian Distribution in Parks and Greenspaces of the Portland, Oregon Metropolitan Area: A Multiple Scale Investigation

Loss of biodiversity due to habitat fragmentation is worldwide problem. With growing human populations and increasing urbanization, it is a necessity to conduct studies on wildlife occurring in urban areas. Currently there is a deficit of research investigating woodland amphibians in urban environments. My objectives were to describe amphibian species richness and abundance in the Portland, Oregon, Metropolitan region, and relate patterns of variation to variables at three increasingly large spatial scales: 1) local microenvironmental (i.e. amphibian/substrate interaction), (2) macrohabitat/patch (i.e. park or greenspace), and 3) landscape (surrounding parks and greenspaces). Environmental variables occurring within the three spatial scales were tested against amphibian species richness and abundance measures using hierarchical partial regression. Ten species were detected in 17 parks and greenspaces. Amphibian distribution was highly nested with the fragmentation resistant species, *Ensatina eschscholtzi*, being most common. The relationships of urban amphibian species richness and relative abundance with environmental variables did not differ greatly from studies conducted in non-urban areas, although

overall capture rate appeared to be much lower. Amphibian species richness was most influenced by macrohabitat/patch scale variables, and was highest at sites that were large, with a high density of high shrubs, low density of low shrubs, and where deciduous trees were dominant. Amphibian abundance varied with a different set of variables and responded most strongly to variation in the forest floor microenvironment. Abundance was highest at sites with cooler, moister soils, where bare soil was common, and cover of fine woody debris was low. Although, found to be insignificant in this study, landscape scale variables, with continuing research, may prove to play a critical role in local population persistence as it relates to a species ability to recolonize fragments and migrate to aquatic breeding sites. To maintain, or possibly increase, species richness and abundance in this area, efforts must be made to promote conditions within the macrohabitat/patch scale that support amphibians. These include preserving the current size of larger parks and greenspaces, increasing the complexity of the tall shrub understory, increasing species richness of the tree community, and maintaining the existing forest patches surrounding parks and greenspaces.

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I dedicate this thesis to Dr. Richard Forbes, from whom I was inspired to become a biologist. His vast knowledge of the subject and his generous and caring nature gave me the confidence to pursue my dreams. I strive to be like him.

I also dedicate this thesis to my friends, family, and colleagues, especially Krey Easton, Amy Dolan, and my advisor Dr. Michael Murphy, without their generous help and support this would not have been possible.

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INTRODUCTION

Continuing declines in biodiversity throughout the world (Meffe and Carroll 1994, Novacek and Cleland 2001, Jenkins 2003) result from many factors, but there is little doubt that land conversion resulting in habitat loss and fragmentation is the leading cause of most losses (Czech et al. 2000, Sala et al. 2000, Collins and Storfer 2003). Fragmentation of contiguous areas create habitats that are smaller, more isolated, and often of lesser quality (Harris 1984). Little progress has been made towards reducing human caused fragmentation of habitats, and therefore understanding the effects of fragmentation on native biotas is essential for the latter's conservation.

Fragmentation is a complex issue because it potentially creates multiple problems that are often species specific. The area of available habitat is immediately reduced, thereby limiting the number of individuals a patch can support. Local extinctions due to disturbances and demographic stochasticity become more likely as population size falls (Fahrig and Merriam 1994). Furthermore, as fragmentation continues and patch isolation increases, the likelihood that a patch of appropriate habitat will be recolonized declines (Blaustein et al. 1994). Fragmentation also increases the probability of loss of species dependant on rare or sparsely distributed habitats, increases exposure of native species to aggressive exotic competitors or predators, and creates edge habitats that are often unsuitable for native species (Saunders et al. 1991).

Ecological studies of fragmented landscapes have historically relied heavily on the theory of island biogeography and emphasized the importance of fragment area and isolation (McArthur and Wilson 1967). Larger fragments are expected to contain more species, and at greater abundances, than smaller fragments. A shortcoming of this perspective is that the land area within which the fragments are embedded (i.e. the matrix) is assumed to be uniformly inhospitable. Two corollaries are that (1) individuals cannot survive in the matrix, and that (2) patch isolation can be measured by the distance between patches. However, the terrestrial matrix is often a mosaic of land cover types, each with differing levels of resistance to movement of individuals between patches. Some habitats of the matrix, although inadequate for reproduction, may provide sufficient resources for nonbreeding individuals. Thus, the internal dynamics of fragmented habitat patches cannot be fully understood without considering the influences of the surrounding matrix.

Recent studies have begun to investigate how the configuration and composition of the landscape matrix affect patterns of diversity in fragmented environments (Fahrig and Merriam 1994, Knutson et al. 1999, Nupp and Swihart 2000, Ricketts 2001). Maserolle and Villard's (1999) review of fragmentation studies found landscape scale variables were significant predictors of vertebrate species presence and abundance 59% of the time. Nonetheless, local habitat features also proved to be of primary importance, especially for taxa with limited dispersal capabilities and strict habitat requirements (e.g. invertebrates and

amphibians). Possibly the most important conclusion of the review (Mazerolle and Villard 1999) was that the distribution and abundance of many species appeared to be determined by multiple factors acting at different spatial scales, and that different taxa often responded differently to variation in local, patch and landscape structure (Ricketts 2001, Welsh and Lind 2002, Mazerolle 2003).

Most fragmentation studies have been conducted in agricultural or forested landscapes. This is especially true for amphibians (Guerry and Hunter 2002, Lowe and Bolger 2002, Houlihan and Findlay 2003). Urbanization, however, is having an increasingly pervasive influence in many landscapes (McKinney 2002), because most of the world's populations now live in urban environments. This trend is expected to continue (United Nations 1993), and indeed the United States population is projected to grow by 50% and become more urbanized over the next fifty years (Hollmann et al. 2000). Moreover, urbanization as a type of land conversion is estimated to exceed population growth by a factor of 6-10 (Richmond 1996), consequently, many currently suitable wildlife habitats will become fragmented and surrounded by an urban matrix, becoming possibly the last refuges for locally occurring native populations.

Effects of habitat fragmentation in urban landscapes are generally more complex, and/or severe, than that found in agricultural or forest settings. For instance buildings and roads, are more abundant and more heavily traveled in urban landscapes, (Blair 1996, Trombulak and Frissell 2000, Carr and Fahrig

2001, McKinney 2002), human contact is higher (Hecnar and M'Closkey 1996, Miller et al. 1998, Malmivaara et al. 2002), and exposure to pollutants (Goldman et al. 1995), domestic pets (Miller et al. 2001) and exotic species are elevated (Moran 1984, Blair and Launer 1997). Additionally, patch configuration and composition within the matrix may be very different in urban areas. Cousins (1982) found that patches in urban areas are usually surrounded by cleared areas, roads, buildings and other man-made environments, and generally become smaller and more isolated toward the urban core. The hospitability of the urban matrix may also differ among taxa. Highly vagile species capable of dealing with a wide range of physical environments (e. g. birds), may be less affected by urban fragmentation than species with weak powers of dispersal and narrow physiological limits (e.g. most amphibians). Studies of birds in urban landscapes have shown that the effects of urbanization vary considerably among species, but in general native bird species diversity declines as urbanization increases (Blair 1996, Hostetler and Holling 2000, Hostetler and Yanez 2003, Melles et al. 2003, Miller et al. 2003). Small mammal communities within urban environments tend to support fewer native species and consist of mostly generalists (VanDruff and Rowse 1986). Mammalian species richness also tends to be negatively associated with urbanization, increased proximity to buildings, and decreased patch area (Dickman 1987, Bolger et al. 1997, How and Dell 2000). Remarkably few empirical studies investigating amphibian environmental relationships have been conducted in urban areas (Beebee 1979, Dickman 1987, Gibbs 1998a, 1998b,

How and Dell 2000). Dickman (1987) showed that amphibian species richness increased with patch area and proximity to permanent water sources in an urban setting. The few other existing studies suggest that built areas and roads can act as barriers to amphibian movements, while residential yards and streambeds increase habitat permeability and dispersal of amphibians between fragments (Gibbs 1998a). Clearly urban areas have not received the intensive study needed to understand the specific environmental forces driving the distribution and abundance of amphibians.

As a group amphibians are highly sensitive to changes in the physical environment and often require specific moist microhabitats for both reproduction and survival (Thorson 1955, Grover 2000). Fully terrestrial salamanders in the family Plethodontidae are also limited by their lack of lungs and reliance on cutaneous gas exchange (Feder 1983). For semi- or fully-terrestrial species, activity periods away from moist retreats are limited by their narrow physical tolerances (Thorson 1955, Heatwole and Lim 1962). Nonetheless amphibians are integral components of many forest ecosystems and play important roles as consumers and prey (Burton and Likens 1975). Indeed Wyman (1998) showed that loss of salamanders increased leaf decomposition rates and reduced carbon storage in forests of eastern North America. Declines of salamanders released invertebrate detritivore prey, thereby increasing rates of leaf litter consumption.

In an effort to fill the deficit in research of amphibian communities in urban environments, I conducted an investigation of amphibian distributions at

multiple spatial scales at 17 parks and greenspaces (P&GS) in Portland, Oregon. My objectives were to (1) describe species composition and relative abundance of amphibians occurring in Portland's urban forest fragments, and (2) examine amphibian-environment relationships at multiple scales to determine whether amphibian species richness and abundance respond mainly to microenvironmental, macrohabitat/patch or landscape features within this urban setting. Increasingly, evidence suggests that studies conducted at multiple spatial scales have the greatest potential for identifying links between biotic diversity and environmental variability and my study is the first to attempt a simultaneous investigation of the effects of environmental variation at three spatial scales on amphibian community structure in any environment.

STUDY AREA

I conducted my work between April 2002 and January 2004. My study area included portions of three counties (Multnomah, Washington and Clackamas) that are located in the northern Willamette Valley in northwestern Oregon. The region has a Mediterranean climate with an average annual precipitation of 94 cm. Winters are characteristically cool and wet and summers warm and dry, 44% of annual precipitation falls mainly as rain from December through February, whereas summer rainfall accounts for only 8% of the annual total (June through August). Winter temperatures do not usually fall below freezing and average annual temperature is 11.8°C (National Climate Data Center online).

The regional vegetation is classified as either Western Hemlock or Willamette Valley (Franklin and Dyness 1973). Most forests falling within the Western hemlock type, although named for the climax species, are dominated by the subclimax Douglas fir (*Pseudotsuga menziesii*) with secondary contributions from western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and grand fir (*Abies grandis*). The understory of the Western Hemlock zone includes salal (*Gaultheria shallon*), oceanspray (*Holodiscus discolor*), western sword fern (*Polystichum munitum*), Oregon oxalis (*Oxalis oregano*), Oregon grape (*Berberis nervosa*), and vine maple (*Acer circinatum*). The relative contributions of the former species all vary with soil moisture. Douglas fir is also common within the

Willamette Valley zone, but deciduous angiosperms such as big leaf maple (*Acer macrophylla*), serviceberry (*Amelanhier alnifolia*), red alder (*Anus rubra*), Oregon ash (*Fraxius latifolia*), and Oregon white oak (*Quarcus garryana*), also contribute heavily.

I selected 17 forested P&GS for study. My choice of P&GS's was based on both my ability to gain permission to use the site and my explicit desire to investigate the interplay between site characteristics (e.g. size and isolation) and amphibian distribution and species richness. All P&GS's were located within the greater Portland, Oregon Metropolitan "urban growth boundary". Potential P&GS's were located on a regional map depicting areas of closed forest canopy. I then used Arc Desktop 8.2 (ESRI 380 New York St. Redlands, CA 92373-8100), and a parks and greenspaces layer provided by METRO's Regional Land Information System (RLIS) to acquire P&GS ownership (city and state ownership was preferred) and site area. I established the suitability of each P&GS by visiting each site to ensure that it was a closed canopy mature second growth forest (50-100 years old) comprised of both deciduous and coniferous trees. To investigate the influence of patch area and patch proximity on amphibian distribution I attempted to include sites of a wide range of sizes (9-1500 ha, Table 1) and varying distances from other patches (Fig. 1). Although all sites fell within a matrix of urban development, it is essential to realize that they were all natural areas capable of supporting complex forest communities. Study sites lacked

manicured areas such as playgrounds and ball fields, and although open to the public, activities (mainly hiking) were limited to designated trails.

METHODS

Pitfall array placements and surveys

I sampled amphibians at each site using terrestrial drift fences with pitfall traps (i.e. pitfall arrays = PFA), and several supplemental methods (see below). The intent of PFA is to intercept amphibians traveling aboveground and to redirect their movements towards traps. PFAs have been shown to increase the likelihood of capturing rare species, and cause less habitat destruction than other methods (Corn and Bury 1990, Adams and Freedman 1999). The latter was an important consideration because nearly all sites were locally protected. Each PFA consisted of three 30 cm tall and 5 m long drift fences made of landscaping cloth buried 5 cm below the ground surface. The three drift fences were arranged in a Y formation (120° between adjacent arms) with one pitfall at the center and one at the end of each arm of the Y (Corn 1994). The pitfall traps were 15 cm radius, 6.6 liter buckets buried such that the rim was flush with the ground surface. Although a PFA was composed of four pitfalls connected by drift fences, I considered a trap night (= TN) to be 1 pitfall operated for 24 hours. I lined the bottom of each pitfall with 1 cm of soil and moss from the surrounding area and a sponge, and at the beginning of each sample period the contents of the buckets were moistened with water. Each pitfall had a plastic lid that served both as a cover to prevent captures when not in use and to shield the pitfall from rain during trapping sessions. Three wooden blocks were attached to the lid's outer surface to elevate the lid 5 cm above the ground surface while the traps were open. To also

prevent flooding of traps, four 3 mm holes were drilled in the bottom to drain accumulated water.

Two PFAs were established at 14 of 17 sites in spring 2002. The remaining three largest sites had three PFA placed within each (Table 1). Given the spatial dimensions of the PFA (10 m diameter circle), and my explicit goal of maximizing amphibian captures with minimum disturbance to the local environments, I selected sample points for PFAs non-randomly by requiring that sampling locations (1) contain vegetation representative of the site, (2) be at least 100 m from the forest canopy boundary and at least 15 m from trails, and that (3) the PFA be compatible with the existing vegetation structure. I avoided areas with extremely steep slopes, open canopies, more than 60% ground cover by English ivy (*Hedera helix*), and sites with high probabilities of being discovered by park visitors. I installed additional PFAs at 10 sites in the spring of 2003 to test whether added sampling effort increased number of captures, generated higher species richness, and to better sample habitat variation within these study areas. Installation of additional PFA at a site was contingent on the existence of locations within the site that met the original guidelines for PFA placement. Mean nearest neighbor distance between PFA within P&GS's was 370 m. With the exception of a single site where distance between PFAs was 49 m, minimum nearest neighbor distance within P&GSs ranged from 83 to 977 m.

Sampling began in October 2002 and continued through January 2004. I sampled each PFA every three weeks for a period of three consecutive days from

October 2002 through December 2002, and again from March 2003 through June 2003. Traps were closed during all non-sampling periods. Seemingly low capture rates during the 2002/2003 field season prompted me to change protocol for the 2003/2004 field season, and I kept all PFAs open for the entire season (first week of October 2003 through the last week of January 2004). All PFAs were checked weekly for captures. One PFA was closed midway through the fall 2003 season because of inaccessibility due to high water. In an effort to minimize small mammal (mainly *Sorex* sp.) mortalities during trapping, I placed a 1 cm diameter stick such that it extended diagonally from the bottom to just beyond the upper lip of the bucket at the ground surface (Perkins and Hunter 2002).

Upon capture, I identified individual amphibians to species, sex, and measured mass to the nearest 0.1 gram and both snout-vent length and total length in mm (total length was measured from tip of snout to the tip of the tail). The animals were then toe clipped. Toe clipping during the fall 2002 season followed a protocol to permit individual identification (Hero 1989), but because of very low recapture rates in 2002 I replaced individual marking by single batch marking in spring 2003. I wiped clippers with 95% ethanol before every use and applied an antibacterial ointment to the clipped toe. Animals were then released at a distance of approximately 1 m outside the PFA in a covered moist location.

Supplemental sampling

Although PFA's effectively sample terrestrial amphibians (Adams and Freedman 1999) they underestimate arboreal species (e.g. *Aneides ferrus*), climbers (e.g. *Hyla regilla*) and species closely associated with streams (e.g. *Plethodon dunni*) or other aquatic habitats. To account for deficiencies of the PFAs, I also recorded all auditory and visual detections of all amphibian species made during scheduled visits to check PFAs. In addition, I conducted one stream survey at all P&GS's with a source of permanently flowing water. The timing of the stream surveys (9-23 July, 2003) ensured adequate but not high water, so that visibility was high, and at a time prior to larval metamorphosis and dispersal (Bury per. com.). Stream surveys were based on a modified method presented by Corn and Bury (1991). I randomly selected one 10 m long section from a 0.1 km section of stream that was divided into ten 10 m lengths. I avoided areas with waterfalls, deep pools and sections that were generally inaccessible. All rocks and logs within the 10 m section on the bank and stream were overturned. A d-shaped dip net was placed downstream of overturned rocks to capture animals, and to sample areas near cracks and overhanging banks. Amphibian captures were recorded to species, sexed and measured as described above. Total search time for each 10 m section was recorded.

Environmental sampling: soil pH, moisture and temperature

To test the hypothesis that local microenvironmental conditions affected capture rates, I collected weekly soil samples within all PFA's to measure soil pH, moisture and temperature from October 2003-January 2004. Sample locations were chosen by randomly picking a number from 1 to 3, and then from 1 to 5, to identify the section and distance (in meters), respectively, from the center of the PFA for soil collection. Soil samples were collected at the humus layer by brushing away the leaf litter layer and other organic matter to expose soil. I then double-bagged approximately 20 g of soil into two resealable plastic bags. Soil temperature was taken at the same time by inserting an alcohol thermometer 3 cm into the mineral soil. In the laboratory, soil pH was measured by creating a slurry of 5 g of soil and 5 g distilled water. The slurry equilibrated for 5 minutes and pH was then measured using a calibrated Orion Research Model 201 Digital pH meter with a VR Scientific Probe. Soil moisture was measured by drying 6 g of soil for 24 hours at 60°C. Dry mass was divided by the initial soil mass and multiplied by 100 to obtain percentage soil moisture.

Environmental sampling: habitat composition and structure

Extensive habitat surveys were conducted at each PFA during July and August of both 2002 and 2003. At each PFA, I placed a 10 m radius circle adjacent to the northernmost pitfall of the PFA. Within each circle, two 20 m transects were aligned north to south and east to west and through the center, and

at every 2 m I measured structure and species composition of shrubs and herbaceous layers and ground cover ($n = 21$ pts/circle). I included woody stems less than 2.54 cm diameter at breast height (DBH) and perennial ferns (mainly sword fern) as shrubs and quantified shrub density by counting the number of contacts with a 3 m long pole divided into 0.5 m increments held vertically at all 21 points. Herbaceous plant ground cover was estimated by measuring the number of plant contacts with a 1 m long stick, divided into 10 cm sections, that was placed horizontally on the ground and perpendicular to the transect at all 2 m sections of the transects. Percentage herb cover was estimated by dividing the number of 10 cm sections with herbs by 10 and then multiplying by 100. Herb species occurring along the 1 m stick were also recorded. Other ground cover variables, including bare soil, moss, rock, small fine woody debris (diameter < 2.54 cm), large fine woody debris (2.54 cm $<$ diameter < 10.00 cm) and leaf cover were also measured at the same locations using the method described for the herbs. Leaf litter depth, not including the duff layer, was measured at the center of the 1m long stick.

The tree community at all PFA was surveyed within the same 10 m radius circle by measuring the DBH of all stems greater than 2.54 cm and recording species. The diameter of logs and snags (all > 10 cm diameter) were measured within the 10 m radius circle and their decay class recorded using Sollin's (1982) scale. Logs or snags of decay class one showed few signs of decay and had intact branches and bark. Decay class two included logs with loose bark and few

branches. Logs in decay class three had no branches and a clean bole. Decay class four showed soft outer wood, and decay class five logs exhibited soft outer and soft inner wood. Volume of wood in each decay class was estimated by multiplying the log or snag length by the cross sectional area. The latter was estimated using the formula for the area of a circle with the diameter based either on DBH (snags) or the measurement taken at the middle of the length of the log. Percentage tree canopy cover was estimated at each 2 m point along the two transects by viewing the immediate overhead canopy through a 3 cm diameter, 10 cm long plastic tube. My study was part of a larger effort to examine the relationship between terrestrial vertebrate diversity and environmental variables in an urban environment, and as a consequence, an additional 31 randomly located, but otherwise identical, vegetation plots were sampled within my 17 sites, generating an average of seven total vegetation plots for each P&GS. The additional vegetation plots were essential for characterizing the structure and composition of the habitat of each site. For more detailed description of methods and procedures used to obtain habitat variables see Lichti et al (submitted).

Environmental sampling: characterization of patch and landscape

Patch refers to an actual park or greenspace, the limits of which were defined by continuous closed canopy forested areas, not traversed by paved roads, and with little to no built area below the forest canopy. Thus, patch boundaries usually extended slightly beyond the legal property limits of the P&GS's.

Landscape refers to the area which extended 1000 m beyond the patch boundary (as defined above). A 1000 m buffer has been used for defining landscape previously in the study of forest fragments (Melles et al. 2003), is large enough to cover most amphibian dispersal (Stebbins and Cohen 1995) and also characterizes habitats abutting the P&GSs. I obtained GIS data sets to characterize and measure patch and landscape variables from the RLIS database. Site boundaries were calculated in Arc Desktop by manipulating the closed canopy layer with a streets layer and a taxlot layer. The closed canopy layer was split by roads and queried to remove tax lots on which more than 5 percent of the land was built. This created a new data layer where sites or patches were defined by areas where closed canopy was not bisected by roads and did not include closed canopied areas with greater than five percent built area.

Following initial processing using Arc Desktop, a combination of patch and landscape coverages were input into Fragstats (McGarigal and Marks 1995) to calculate biogeographic patch metrics including size and shape. The latter was measured by a shape index wherein a value of 1.0 represents a perfect square. The shape index increases above 1.0 as fragments become less Euclidian (i.e. relatively greater edge compared to the internal volume). I also used Fragstats to measure proximity to other habitat patches (the sum of patch *i* area divided by the square distances between patch *i* and the focal patch for all wooded areas in the 1000 m buffer), and stream and wetland density within each patch. The two latter variables were calculated by dividing the area of each by the total area (ha) of the

patch, and then multiplying by 100. Landscape variables used in analyses were quantified within the buffer surrounding each of the study sites, and consisted of the percentage of the 1000 m wide buffer covered by forest, built forest (closed canopy with greater than 5% of the underlying area made up of buildings), single family residential, multifamily residential, industrial/commercial, agricultural, or public/open spaces. Following initial queries in Arc Desktop using a tax lot layer, percentage cover of land use categories stated above within the 1000 m buffer were obtained through Fragstats analysis for each of the P&GS's. Values for population, road, and building density were calculated using Arc Desktop. The number of people, roads, and buildings within the buffer were divided by the area (ha) of the 1000 m buffer surrounding each P&GS. Digital elevations models (DEMs), obtained through the Metro GIS department, were used to calculate elevation (the average elevation within the 10 m radius circle), slope (the average slope within the circle), and potential relative radiation (PRR), a solar radiation measure which accounts for both temporal variation and topographic shading by adjacent landforms. To obtain estimates of PRR I calculated hourly hillshaded radiation grids by using the hillshade function in Arc Desktop applied to site DEMs, solar azimuth, and solar inclination (Pierce et al. 2004). PRR sums hourly estimates of radiation over the day and then sums the daily values over a year creating a relative measure of radiation relevant to vegetation and other organisms that respond strongly to temperature and moisture. For more detailed description

of methods and procedures used to obtain landscape variables see Lichti et al (submitted).

Statistical analyses

PFA sites and other vegetation sampling points were chosen using different criteria and it was possible for the vegetation to differ between these sites. I tested for this possibility using an ANOSIM test, a non-parametric, permutation based procedure analogous to ANOVA. Based on Bray-Curtis distances and 999 permutations I found no significant difference between PFA sites and randomly located vegetation plots (vegetation structure $r = -0.062$, $P = 0.946$; floristic composition: $r = -0.062$, $P = 0.961$). My PFA sites were thus representative of the vegetation found within the respective P&GS's.

Detection probabilities of amphibians are often low and usually vary temporally because activity periods are highly seasonal, and often vary with weather, habitat, and population density (Bailey et al. 2004). Given this, I felt that it was prudent to combine data from both years to characterize a site's amphibian community rather than conduct analyses on each year individually. Nonetheless, to evaluate the extent to which species may have been missed if I had conducted briefer sampling efforts, I compared species detection probabilities for each species (number of dates captured/ total number capture opportunities) across seasons and between the two years of different sampling regimes.

I based my estimates of species richness on combined results of all survey methods (PFAs, vocal/visual encounters during visits, and stream surveys). All

P&GSs were visited an equal number of times and therefore the probability of chance encounters was roughly equal across sites. On the other hand, sites varied in the number of trap nights due to differences in the number of PFAs and the necessity to close one of the PFAs midway through the 2003 fall season. I therefore standardized my estimates of pitfall array richness and capture rates to 1000 TNs by dividing each variable by the number of TNs and multiplying by 1000. The dependent (i.e. response) variables for my analyses thus included total species richness, standardized capture rates from the pitfall arrays, standardized abundance of *Ensatina eschscholtzi*, the most widespread and abundant amphibian in our sample, and standardized abundance of amphibians other than *Ensatina eschscholtzi*.

Nested-subset theory (Patterson 1986) describes species assemblages where species poor patches (e.g. islands or habitat fragments) support a subset of the species found in species rich patches. Because of poor dispersal capabilities of amphibians, fragmented habitats where amphibians occur often show a nested subset distribution of species (Wright et al. 1998). The nestedness calculator (Atmar and Patterson 1995) was used to calculate an index of nestedness based on amphibian presence/absence for all P&GSs. The nestedness calculator maximally packs the community and then calculates the matrix wide nestedness value. The latter varies from 0° system to 100° for perfectly nested and completely random systems, respectively. Monte-Carlo simulations (100) were then used to generate random matrices where the number of occupied cells was held constant based on

the observed presence/absence matrix. System temperature of the observed and simulated communities were compared using a Z-test.

I used principal components analysis (PCA: based on correlation matrices) to derive composite variables that summarized the major gradients of environmental variation at the microenvironment, macrohabitat/patch, and landscape levels. I retained principal components for use as variables in later regression analyses (see below) only if eigenvalues were ≥ 1.0 , and I interpreted the axes using the general rule that the contributions of variables with factor loadings of absolute value 0.32, 0.45, 0.55, 0.63, and 0.71 were poor, fair, good, very good and excellent, respectively (McGarigal et al. 2000). All variables were tested for conformance to assumptions of normality, and appropriate transformations applied when necessary. To reduce problems of collinearity among variables, I inspected all possible correlations among variables within a spatial scale (e.g. landscape) prior to the PCAs and eliminated 1 of 2 variables when the correlation between them exceeded an absolute value of 0.70. PCA requires, as a rule of thumb, 3 to 4 cases for every variable included in the analysis. I therefore based my PCAs of microenvironmental and macrohabitat/patch analyses on the 47 individual PFAs and 120 vegetation plots, respectively, located within the 17 study sites (Table 2). However all regression analyses were based on average P&GS scores for all variables.

Variables in the microenvironmental analysis of forest floor characters (Table 2) included traits that had a potential influence on amphibians as a result of

either direct contact with the site, or by affecting availability of shelter (e.g. coarse woody debris). Hence, I included soil temperature, moisture and pH in one PCA, ground cover types in a second PCA, and volume of coarse woody debris (logs and snags) in a third PCA as important potential influences on amphibians at the microenvironmental level. The three PCAs generated seven composite variables from the original 18 variables (Table 2), including three ground cover variables, two soil physical/chemical axes, and two axes summarizing coarse woody debris (logs and snags).

Macrohabitat/patch variables included physical descriptors of the P&GS such as total area, shape, proximity to other wooded sites, elevation, slope and PRR (Table 1). Stream density (m^2 of stream/P&GS area), and the proportion of the P&GS that was classified as wetland (m^2 of wetland/P&GS area), were included as separate macrohabitat/patch variables because of the potentially important amphibian habitats offered by both habitat types (Table 1). A PC analysis at the macrohabitat scale was based on plant structural features that *a priori* predicted would be important for amphibian richness and abundance (Table 3). Thus, density of vegetation in the shrub layer (divided into six 0.5 m intervals), percentage canopy cover, and the overall importance values of angiosperm and coniferous trees were included as macrohabitat/patch variables. Nearly 88% of the among-site variation in the latter traits was summarized by the first four axes of the PCA, and the derived axes 1, 2, 3, and 4 described gradients in density of high shrubs, density of forest canopy cover, density of low shrubs,

and relative importance of angiosperm and coniferous trees, respectively (Table 3).

PC analyses of landscape were conducted using percent land cover type including forest, built forest, commercial/industrial, open space, single family residential, multi-family residential, combined single and multi-family residential, plus several descriptive measures such as population, street and building densities, within the 1000 m buffer surrounding the P&GSs (Table 4). Because PCA of the landscape variables was part of a larger terrestrial vertebrate diversity study that was based on a total of 48 sites, factor loadings were not calculated for the specific amphibian study sites. Instead, I calculated and report (Table 4) correlation coefficients between individual landscape variables for the 17 amphibian P&GS's and the three landscape PC variables derived from the PCA of all 48 sites. Correlation coefficients and factor loadings were extremely similar and yielded identical interpretations. The first landscape PC (LAND1) described a strong urbanization gradient. Sites with negative scores had a high proportion of the buffer covered with forest, and were in close proximity to other forest patches. Both features declined gradually as the buffer around P&GSs showed increases in building, population, and residential housing density (positive scores, Table 4). The second landscape PC (LAND2) contrasted sites with large amounts of built forest with other sites with buffers dominated by open areas. The third landscape PC (LAND3) described a contrast of sites with

abundant residential land use cover (negative scores) with sites zoned for commercial/industrial land uses (positive scores).

My approach winnowed the original 44 variables down to seven microenvironmental, 12 macrohabitat/patch and three landscape variables (Table 5). I used the 22 variables in hierarchical partial regression (Lichstein et al. 2002) analyses of total species richness (= TSR; all methods combined), standardized capture rates from the pitfall arrays (= SCR), standardized abundance of *Ensatina eschscholtzi* (= SCRE), the most widespread and abundant amphibian in our sample, and standardized abundance of non-*Ensatina eschscholtzi* (= SCRNE). Prior to additional analysis I conducted trend surface analysis of all dependant variables to test for spatial autocorrelation of variation by conducting stepwise regressions against the full third-order polynomial of UTM coordinates from the center of all P&GSs. None of the dependant variables were spatially autocorrelated and, therefore, I was able to ignore spatial autocorrelation in subsequent analyses (Legendre 1993, Knapp et al. 2003).

The hierarchical partial regression analyses evaluated the contributions of microenvironmental, macrohabitat/patch, and landscape variables to differences in TSR, SCR, SCRE, and SCRNE. In hierarchical partial regression, variation in dependent and independent variables that is due to another set of variables is removed by partialing the shared variation out through regression (Zar 1999). I conducted my analyses by first assessing the relative importance of variables at each of the three spatial scales by conducting three separate stepwise regressions

(backward elimination, P -to-enter and $-remove \leq 0.05$) of the dependent variable against microenvironment, macrohabitat/patch, and landscape scale characters. This was an important measure to reduce bias caused by initiating the hierarchical partial regression with a predetermined spatial scale. Instead, this approach allowed for the scale accounting for the most variation in the dependant variable to be the starting point of the hierarchal partial regression model. Residuals were calculated for the regression with the highest R^2 . I then tested and corrected for variation between the independent variables that entered the latter regression and the independent variables at the other spatial scales (backward selection, P -to-enter and $-remove \leq 0.05$). This was followed by a second regression between the residuals of the dependent variable from the first regression, and the corrected independent variables at the other two spatial scales. The procedure was repeated before testing for an association between the dependent variable and the remaining scale variables. I also conducted a full stepwise regression of the dependant variables (forward selection, P -to-enter and $-remove \leq 0.05$), using all 22 microenvironment, macrohabitat/patch, and landscape variables, to compare findings from the hierarchical partial regression and the more traditional stepwise regression. Standardized regression coefficients (b) are reported for all variables that were retained as significant predictor variables. All statistical tests were performed using either STATISTIX 8.0 (Analytical Software 2003) or SPSS 11.5 (SPSS Inc. 2002). Additional tests are described in the Results.

RESULTS

Species composition, relative abundance, and detection probabilities

Over three field seasons from October 2002 through January 2004, I captured 299 amphibians of 9 species (3 anurans and 6 urodeles) over a total of 22,948 PFA trap nights (detailed capture records summarized in Appendix A, and B). Stream surveys yielded one additional species (*Plethodon dunni*, Dunn's salamander), increasing total species richness to 10. *E. eschscholtzi* (Oregon *Ensatina* = *Ensatina*) was distributed ubiquitously, being captured a total of 140 times at all 17 P&GSs. The second most commonly captured species was *Taricha granulosa* (rough skin newt) with 80 PFA captures, 75 of which occurred at a single site (Tualatin Hills Nature Park). The remaining 5 captures occurred at 2 sites. The third most commonly captured species was *Plethodon vehiculum* (western redback salamander) with 44 captures occurring among six sites. *Ambystoma macrodactylum* (long-toed salamander) was captured 19 times at three sites and *Rana aurora* (red-legged frog) was captured eight times at two sites. Rarely captured species included *A. gracile* (northwestern salamander), *Dicamptodon tenebrosus* (Pacific giant salamander), *Hyla regilla* (Pacific tree frog), and *Rana catesbeiana* (bullfrog) each of which was caught less than four times at only 1 to 2 sites. I made only five recaptures during the course of this study so no further analysis of mark/recapture abundance was conducted.

Detection probabilities, which were calculated as the number of times a species was detected at a site divided by the number of visits per season, were

only calculated for a species at a particular P&GS if that species was detected at the site at least once (fall 2002, spring 2003, or fall 2003). With the exception of the least frequently detected species, mean detection probabilities for individual species tended to be lower for 5 of 7 species during spring 2003 than fall 2002 (Table 6). Three species detected in fall 2002 were not detected in spring 2003, but one new species was added. Detection probabilities continued to drop or remain low in fall 2003. Nonetheless, all species detected previously (fall 2002 and spring 2003) were detected in fall 2003, and a new species was encountered.

Total species richness (TSR) at each site combined data obtained through PFA sampling, opportunistic visual/auditory detection, and stream surveys (Table 7). TSR averaged 3.2 species/site, but ranged from 1 species (3 P&GSs) to 7 (Tualatin Hill Nature Park =THNP). Pacific tree frog was most commonly "captured" through opportunistic visual/ auditory detections (captured only once in a PFA). Dunn's salamander was never captured during the course of PFA sampling and was only sampled during stream surveys.

Community patterns: area relations and nested subsets

Total species richness (\log_{10} TSR) varied positively, but not significantly, with P&GS area (\log_{10}) ($R^2 = 0.132$, $df = 15$, $P = 0.152$). However, failure to achieve significance appeared to be due primarily to the low richness detected at the largest site (Fig. 2A). Reanalysis after omitting this one point yielded a significant relationship between richness and area ($R^2 = 0.272$, $df = 14$, $P = 0.038$)

with an exponent of 0.238. P&GS proximity, a general measure of patch isolation, gave no suggestion of having an affect on TSR ($P = 0.325$; Fig. 2B). Multiple regression of TSR against both area and proximity did not improve the relationship between TSR and proximity ($P = 0.917$).

The urban amphibian community (table 7) exhibited a highly ordered and nested pattern (Fig. 3), with a system "temperature" of 8.9° . The mean temperature of 100 randomly assembled and geographically isolated systems based on the same data gave a mean system temperature of 45.0 (SD = 8.06), indicating that species were not ordered randomly among P&GS. The temperature calculator suggested that two species were moderately idiosyncratic (*Plethodon vehiculum* and *Rana catesbeiana*: species 2 and 10 from the left in Fig. 3), and that one fragment was particularly idiosyncratic (Tualatin Hills Nature Park [THNP]: 2 from the top in Fig. 3). The position of Forest Park North, THNP and Mt. Talbert in positions 1, 2, and 3, respectively, from the top suggested that they were the most "hospitable" P&GSs.

Covariation among microenvironment, patch and landscape variables

Relatively few strong correlations existed among variables, either within or among spatial scales. Of the 231 possible correlations among all 22 variables, only 5 (2.1 %) and 12 (5.2 %) respectively covaried strongly enough to account for at least 50% (i.e., $R \geq |0.707|$) and 33% (i.e., $|0.576| < R \leq |0.707|$) of each other's variation (Table 8). LAND1 correlated with five variables, and the

pattern indicated that urban landscapes (positive scores on LAND1) were associated with P&GSs that were small, isolated, had little low shrub density, abundant cover of bare soil, and soils that tended to be warm and dry. P&GSs with high proximity scores (i.e. located near other forest sites) tended to be in undeveloped, relatively unurbanized landscapes, were large, and tended to have a more complex edge (i. e. high shape scores) (Table 8). Of the remaining correlations, the two strongest were positive relationships of AREA with STREAM and ELEVATION with MACROHAB4. The former indicated that sites with greater area had the highest density of streams, while that latter indicated that higher density of coniferous trees occurred at sites that were at higher elevations (Table 8).

Multiscale analysis of Total Species Richness

Separate stepwise regression analyses of TSR against each of the three spatial scales indicated that TSR exhibited no relationship with microenvironmental scale variables, but that LAND2 accounted for 29.7% of the variation in TSR ($F = 6.345, P = 0.024$). Four macrohabitat/patch variables accounted for 71.6% of the variation in TSR ($F = 11.072, P < 0.001$), and indicated that richness increased as MACROHAB1 ($b = 0.373, P = 0.017$), and AREA increased ($b = 0.390, P = 0.044$), but declined with both MACROHAB3 ($b = -0.596, P = 0.002$), and ELEVATION ($b = -0.483, P = 0.010$). After partialing out the effects of the four significant macrohabitat/patch variables out of TSR,

and both the microenvironmental and landscape variables, no further associations were found. Thus, the hierarchical partial regression indicated that TSR varied directly with the density of high shrubs (MACROHAB1; Fig. 4a) and area (AREA; Fig. 4b), inversely with the density of low shrubs (MACROHAB3; Fig. 4c), and elevation (ELEVATION; Fig. 4d). A full stepwise regression of all microenvironment, macrohabitat/patch, and landscape variables against TSR resulted in a different model. MACROHAB3 ($b = -0.750$, $P = 0.000$) was retained as significant predictors of TSR, but SOIL1 ($b = 0.402$, $P = 0.009$) and MACROHAB4 ($b = -0.443$, $P = 0.005$) were included instead of MACROHAB1, ELEVATION, and AREA. The three variable model accounted for 73.8% of the variation in TSR ($F = 16.040$, $P = 0.000$). The hierarchical partial regression and full stepwise regression models explained similar levels of variation in TSR, yet only a single variable selected by the two approaches was the same, and in this instance the full stepwise model yielded a slightly higher R^2 . On the basis of the full stepwise regression species richness was highest at sites with low scores for low shrub density, where deciduous trees were dominant, and where soils were relatively more acidic. The replacement of MACROHAB1 with SOIL1, and ELEVATION with MACROHAB4 was perhaps not surprising given the high correlation between these variables (Table 8)

Given that THNP was identified as idiosyncratic by the nested subsets analysis (see above; supported by capture rates that were significantly higher than all other P&GSs, see below), I conducted a second hierarchical partial regression

analysis without THNP. None of the microenvironment or landscape variables varied significantly with TSR. In contrast, six macrohabitat/patch variables made strong contributions to variation in TSR ($R^2 = 0.872$, $F = 17.996$, $P = 0.00$). As before, TSR increased with MACROHAB1 ($b = 0.268$, $P = 0.019$), MACROHAB3 ($b = -0.575$, $P = 0.000$) and AREA ($b = 0.532$, $P = 0.010$), but additionally TSR increased with SLOPE ($b = 0.743$, $P = 0.004$) and decreased with both MACROHAB4 ($b = -0.766$, $P = 0.000$) and STREAM ($b = -0.680$, $P = 0.014$). None of the microenvironmental or landscape variables, when controlled for covariation with macrohabitat/patch variables, entered the regression of residual TSR. A single stepwise regression with all microenvironmental, macrohabitat/patch, and landscape variables resulted in the entry of only one variable, MACROHAB3 ($b = -0.693$, $P = 0.003$). The variation in TSR accounted for by the latter model ($R^2 = 0.481$, $F = 12.967$, $P = 0.003$) was only 55.1% of that explained by the hierarchical partial regression model (see above), suggesting that the hierarchical partial regression model was superior. Thus, based on the hierarchical partial regression results, TSR was highest at sites where there was a high density of high shrubs, a low density of low shrubs, a greater proportion of deciduous trees, at P&GS's that were larger, with increased topographic relief (i.e. positive scores for SLOPE), but few streams.

Multiscale analysis of capture rate

The following analyses were based on captures from PFAs (standardized to 1000 trap nights) averaged across all seasons (standardized capture rate = SCR). My initial analyses of SCR showed that no microenvironment, macrohabitat/patch, or landscape variables had significant associations with SCR. Furthermore a single stepwise regression including all microenvironmental, patch, and landscape variables accounted for none of the variation in SCR.

Capture rates at THNP were significantly higher than other sites (THNP = 68.8 captures/1000 TN, mean capture rate of 13.2 captures/1000 TN for other sites), and as described above, THNP seemed to have unusually high species richness. I therefore eliminated THNP from the analyses to help identify correlates of capture rates at the remaining P&GSs. Three microenvironmental variables emerged as significant contributors to differences in SCR ($R^2 = 0.626$, $F = 9.377$, $P = 0.002$). High capture rates were associated with low scores on COVER1 ($b = -0.605$, $P = 0.003$), high scores on SOIL2 ($b = 0.456$, $P = 0.015$), and low scores on COVER2 ($b = -0.475$, $P = 0.011$). None of the variation in SCR was related significantly to macrohabitat/patch variables, either before or after removing the effects of the three microenvironmental variables. Similarly, after partialing out relationships between the three microenvironmental variables and landscape variables, I found no relationship between landscape and capture rate. Hence, local microenvironmental conditions appeared to be the dominant factors affecting amphibian capture rate and the highest capture rate occurred at

sites with little ground cover (i.e. a high proportion of bare soil), little fine woody debris, but where soils were cool and moist. However, a full stepwise regression of all microenvironment, patch and landscape variables yielded a slightly different picture. The resulting two-variable model of COVER1 ($b = -0.770$, $P = 0.003$) and WETLAND ($b = -0.532$, $P = 0.023$) explained 46.6% of the variation in total capture rate ($F = 7.535$, $P = 0.007$), but oddly, capture rate varied inversely with wetland density.

Ensatina captures comprised 47% of all PFA captures, and as a consequence, our results were possibly affected heavily by this one species. I therefore performed separate analyses of *Ensatina*, and then, all other captures of amphibians. At the microhabitat level, *Ensatina* captures varied inversely with COVER3 ($b = -0.514$, $P = 0.019$), COVER1 ($b = -0.446$, $P = 0.032$) and SOIL1 ($b = -0.459$, $P = 0.036$), and directly with COVER2 ($b = -0.448$, $P = 0.029$). Nearly one half ($R^2 = 0.482$, $F = 4.718$, $P = 0.016$) of the variation in *Ensatina* capture rate was accounted for by microhabitat variables, compared to 0 and 24% ($R^2 = 0.243$) by macrohabitat/patch and landscape scale variables, respectively. At the landscape scale, *Ensatina* captures varied inversely with LAND2 ($b = -0.493$, $P = 0.044$, i.e. low captures at P&GSs surrounded by non-forest open space). Given that the variation in *Ensatina* captures accounted for by the microenvironmental variables exceeded that of the patch, and landscape, I controlled *Ensatina* captures, and macrohabitat/patch variables for the four microenvironmental variables. Upon reexamination, *Ensatina* captures varied

directly with two macrohabitat/patch variables. The joint variability of *Ensatina* captures arising from four microhabitat and two macrohabitat/patch variables indicated that high *Ensatina* capture rate was associated with COVER2 ($P = 0.005$), PROXIMITY ($P = 0.047$) and MACROHAB1 ($P = 0.035$), whereas low capture rates were linked to SOIL1 ($P = 0.012$), COVER3 ($P = 0.006$), and COVER1 ($P = 0.034$). The six variables explained 68.4% of the variation in *Ensatina* capture rate ($F = 6.766$, $P = 0.004$). *Ensatina* were abundant at sites at which little ground cover existed (i.e. a high proportion of bare soil cover, and a low proportion of both small and large fine woody debris, and herbaceous cover), where soils tended to be less acidic, but at P&GSs that had more high shrub cover, and that were also in close proximity to other forested sites. Landscape variables did not enter the regression after controlling for the six microenvironment and patch variables. A stepwise regression of the full set of variables, conducted without controlled entry of specific blocks of variables, selected one landscape variables and accounted for 24.3% of *Ensatina* captures ($F = 4.825$, $P < 0.044$). Capture rate was inversely related to LAND2 ($b = -0.493$, $P < 0.044$), and suggested that P&GSs with the highest *Ensatina* abundance were set in a landscape covered by forest and built forest.

Non-*Ensatina* capture rates were independent of microenvironment, macrohabitat/patch and landscape variation when all 17 sites were examined. However, captures at THNP were significantly higher than at all other sites (THNP = 66.8 non-*Ensatina* captures/1000 TN, versus 6.9 non-*Ensatina*

capture/1000 TN at other sites), and after removal of THNP, I found that at the microenvironment variable non-*Ensatina* captures varied negatively with COVER2 ($b = -0.597$, $R^2 = 0.356$, $P = 0.015$). At the macrohabitat/patch scale, SCRNE varied negatively with ELEVATION ($b = -0.584$, $P = 0.037$) and positively with SLOPE ($b = 0.663$, $P = 0.021$), but accounted for less variation ($R^2 = 0.294$, $F = 4.122$, $P < 0.041$) than the single microenvironment scale variable. I removed the effects of covariation between COVER2 and macrohabitat/patch, and landscape variables, which resulted in no further association of residual SCRNE with variables at either of the two other scales. The full stepwise regression ($n = 22$ variables) confirmed the above analysis in indicating that non-*Ensatina* capture rate increased with decreases in COVER2, accounting for the same proportion of variation as above ($b = -0.597$, $R^2 = 0.356$, $P = 0.015$). Capture rate of amphibians other than *Ensatina* were lowest at sites with a high proportion of ground covered by small and large fine woody debris.

DISCUSSION

Terrestrial woodland amphibian communities within urban environments are poorly studied, and my research represents one of the first such analyses of any city in the United States. I detected 10 species of amphibians in 17 forested P&GS's. Making allowances for special habitat needs, I recorded 10 of the 12 species that could reasonably be expected to be found within the Willamette Valley. The missing species included western toads (*Bufo boreas*) and clouded salamanders (*Aneides ferrus*) (Nussbaum et al. 1983). The former species is missing for unknown reasons from most of the Willamette Valley (Nussbaum et al. 1983), whereas the latter may be difficult to detect without intensive log sampling (Corn and Bury 1991). Otherwise, the proportion of P&GSs occupied by different species, and their ranked order of abundance, appears to be consistent with data derived from studies conducted in non-urbanized landscapes within the region (Aubry and Hall 1991, Gilbert and Allwine 1991, Grialou et al. 2000). *Ensatina*, the most widespread and abundant species encountered, occurred at all 17 P&GSs, followed by western red-back salamanders (6 P&GSs), and rough-skin newt and long-toed salamander (both occurring at 3 P&GSs).

Few meaningful comparisons of capture rates were available because my study was the first to use PFAs in an urban environment. Regional differences in faunal diversity further complicate the picture. However, Bury and Corn (1987) operated PFAs of similar design in 30 forested stands within the Cascade Range of western Oregon and Washington for 180 days from the last week of May to

late November, 1983. My fall 2003 field season (122 day) yielded a capture rate of 7.9 captures/1000 TNs, which was dramatically lower than 31.8 captures/1000 TNs obtained from Bury and Corn (1987). Capture rates for the commonly occurring species, *Ensatina*, was similar to rates reported for the Oregon Coast Range by McComb et al. (1993) in red alder stands and by Corn and Bury (1991) in Douglas fir stands, while western red-back salamander capture rates were similar and lower, respectively. Although conclusions must be made cautiously, these data suggests that fragmented P&GSs within an urban landscape are similar in species composition to non-urbanized sites, but that they may support fewer individuals than areas of relatively continuous forested habitat within non-urban landscapes.

Amphibian Environmental Relationships

The only studies of which I am aware that have addressed questions concerning woodland amphibian distribution and or movement in largely terrestrial urban settings are Dickman (1987), Gibbs (Gibbs 1998a, b), and How and Dell (2000). Dickman's (1987) study of residual vegetation patches of various habitat types in the city of Oxford, England, showed that amphibian and reptile species richness was positively associated with patch area and proximity to permanent sources of water (30% of species richness variation was accounted for by these two variables). Gibbs conducted two investigations, one in which he found a reduction in site occupation by certain woodland amphibians as canopy

levels fell below thresholds of 30% and 50% along an urban to rural gradient (Gibbs 1998b). Gibbs' second investigation (1998a) was of a 1000 ha forest that was surrounded by residential areas, golf courses, and roads and highways. He found that movement of woodland amphibians was facilitated by certain landscape features (streambeds and forest edge associated with open lands), and hindered by others (forest-residential and forest-road edge). How and Dell's (2000) study of vegetation remnants in Perth, Australia, demonstrated no significant relationships between species richness and remnant area, and additionally, found no regional patterns associated with species richness and the underlying soil type.

Amphibians of the Portland Metropolitan area exhibit a highly ordered and nested distribution pattern. Nested-subset distribution results from selective extinction (i.e. "faunal relaxation") or selective immigration. "Relaxation" is the process by which communities within fragmented landscapes lose fragmentation and/or area sensitive species that once existed in the previously contiguous area. P&GSs in Portland showed higher abundances of non-fragmentation, non-area sensitive species, presumably as a result of faunal relaxation. Sedentary species tend to be the most fragmentation resistant, whereas highly vagile species that depend on multiple habitats to complete their lifecycles tend to be most sensitive to habitat loss from fragmentation (Gibbs 1998b). *Ensatina*, with its small home range, lack of seasonal migration (Stebbins and Cohen 1995), and tolerance for dehydration (Ray 1958), appears to have been the most fragmentation resistant

species (Table 7). The temperature calculator suggested that the western red-back salamander was moderately idiosyncratic despite exhibiting a small home range, lack of seasonal migration and presence at a high proportion of sites. Idiosyncratic distribution may result from (1) post-isolation immigration, (2) competitive exclusion, (3) historical disjunction, and (4) requirements for a specific environment (Atmar and Patterson 1993). Western red-back salamander may be capable of maintaining local populations following fragmentation but their distribution may be a consequence of either a geographically disjunct historical range or inability to recolonize sites following local extinction. The temperature calculator also suggested that the bullfrog was a moderately idiosyncratic species. A possible explanation is that bullfrogs, being a relatively recently introduced species, is still in the process of dispersing to P&GSs, and has yet to become a fixture at any of the sites. Alternately, its pond-breeding habit may create a naturally spotty distribution. THNP was an idiosyncratic P&GS. This was partially a result of the presence of bullfrogs at the site, but may also be explained by the higher proportion of other pond breeding species (rough-skin newt, long toed salamander, northwestern salamander, and red-legged frog), and a distinctive habitat that differed from other sites (Lichti et al 2004).

Predictors of Richness and Abundance

I conducted my analyses of amphibian-environment relationships using a traditional stepwise regression model in which all variables were allowed to enter,

and the more structured hierarchical partial regression approach. The use of hierarchical partial regression accounted for equivalent or larger amounts of the variation in 4 out of 5 analyses, but for the most part, the two approaches yielded similar results. My analysis demonstrated that landscape variables never entered the analyses using hierarchical partial regression, most likely because landscape had indirect effects on variables measured at the two finer scales. A single landscape variable entered the unrestricted stepwise regression of *Ensatina* (LAND2), but its statistical significance probably arose from covariation of landscape variables with microenvironment and macrohabitat/patch variables (Table 8).

My results showed that total species richness responded primarily to macrohabitat/patch variables, but that amphibian abundance varied mainly with microenvironmental variables describing ground cover and soil features. This suggests that species richness is largely a function of macrohabitat vegetation structure and geophysical patch characteristics, and to a lesser extent, the species composition of the dominant vegetation (i.e. conifers vs. angiosperms). Standardized capture rates (~ amphibian abundance), on the other hand, appear to be contingent on the existence of favorable conditions at the ground level of the forest. As stated previously, landscape variables never contributed to the variation in any of the dependant variables in the hierarchical partial regression. Thus, the landscape appeared to have little influence on amphibian distribution and abundance within an urban setting. However, one macrohabitat/patch

variable that contributed to variation in *Ensatina* capture rates arguably incorporates a landscape trait. PROXIMITY, or the proximity of the P&GS to other forested patches is the buffer, varied positively with *Ensatina* capture rates. Although centered on the individual P&GS, PROXIMITY reflects connectivity of forested sites within the 1000 m buffer. Hence *Ensatina* was more abundant when forested patches in the landscape buffer were better connected.

Landscape scale variables may have emerged as less important than variables from the other two finer scales as a consequence of the current species assemblage. As stated previously the system appears likely to have already undergone faunal relaxation, and the communities are composed mainly of fragmentation resistant species. The P&GSs are thus inhabited mostly by species that do not require extremely large areas or specific aquatic breeding sites, leaving them relatively immune to changes in the surrounding landscape composition and configuration. Consequently, I cannot discount landscape as an important factor influencing amphibian community dynamics. Landscape composition and configuration are still vital for local population persistence for both vagile species that must traverse the matrix to seasonally migrate to breeding sites, and those less vagile species that, although fragmentation resistant, will lack the ability to traverse large areas of inhospitable matrix to recolonize a site following local extinctions.

Although identification of the spatial scale (microenvironment, macrohabitat/patch, and landscape) that accounts for most of the variability in

amphibian community structure is extremely important, it is also valuable to document the specific variables accounting for the bulk of the variation in amphibian richness and abundance. Amphibian species richness of forest fragments within an urban environment was associated with increased P&GS area, increased tall shrub density, decreased low shrub density, and decreased elevation. With THNP removed from the analysis, species richness was associated with the initial three variables from above, but was additionally higher at sites with greater topographic relief, a higher proportion of deciduous trees, and at sites with lower stream densities. Area, a common correlate of increased amphibian species richness in non-urban landscapes (Houlahan and Findlay 2003, Mazerolle 2003, Silva et al. 2003) proved to be a significant positive correlate of species richness in P&GSs of the Portland Metropolitan area, even after accounting for variation in macrohabitat structure and elevation. Availability of water, another common correlate of increased species richness has been associated with high species richness in both urban (Dickman 1987) and non-urban areas (Corn and Bury 1991, Marsh and Pearman 1997, Mitchell et al. 1997). I failed to detect a positive association of streams and wetlands with species richness. This may reflect the general lack of permanent water at nearly all of my study sites, and additionally may be a consequence of the current species assemblage, nine of which do not require streams to breed (Nussbaum et al. 1983).

Total amphibian abundance within urban forest fragments was strongly associated with variables of the microenvironment scale. The forest floor at sites with higher amphibian abundance had a relatively high proportion of bare soil, relatively low amounts of fine woody debris, but soils at these P&GSs tended to be relatively moist and maintain low temperatures. Hierarchical partial regression analyses of both SCR and SCRE had increased cover of bare soil (- COVER1) enter the model. This may be a consequence of *Ensatina* and western red-back salamander habitat requirements. Combined, these two species accounted for 67% of all captures, with *Ensatina* reported to vary positively with increased cover of bare soil (Gilbert and Allwine 1991), and western red-back salamanders commonly found in coniferous forest habitats where leaf litter cover and depth tends to be low (Nussbaum et al. 1983). The positive association of total capture rate with high soil moisture content has been detected in other studies of amphibians (Hyde and Simons 2001). The significantly negative correlation between LAND1 and SOIL2 (Table 8) indicating that soils of P&GSs surrounded by an urbanized matrix tended to be warm and dry, along with reported negative effects of fragmentation on soil moisture (Saunders et al. 1991), suggests that fragmentation could be extremely detrimental to amphibians within highly disturbed and patchy urban environments. Many studies from non-urban areas in eastern North America have documented the negative effects of soil acidity on the distribution and behavior of amphibians (Wyman 1988, Wyman and Jancola 1992, Sugalski and Claussen 1997). Soil pH did not enter the hierarchical partial

regression of amphibian captures in Portland, but the pH levels that I documented (mean site pH ranged from 5.5 to 6.5 ($[H^+]$) were well within the tolerable range for amphibians. Large coarse woody debris (i.e. logs and snags) is often suggested to be a limiting resource, because of the cover, foraging, and breeding sites that it provides for salamanders (Bury et al. 1991, Corn and Bury 1991, Dupuis et al. 1995). Surprisingly coarse woody debris measures (CWD1 and CWD2) did not enter any of the hierarchical partial regression analyses.

Ensatina was distributed ubiquitously, among all 17 P&GSs and its abundance was associated with increased bare soil, low cover by fine woody debris, higher soil pH, increased density of high shrub, and increased proximity to other forest fragments. *Ensatina* abundances were correlated with higher soil pH, suggesting *Ensatina* prefers a more neutral soil pH approaching 6.5. Of most interest was the association of increased abundance at P&GSs with high proximity scores, supporting the findings of Demaynadier and Hunter (1998) that small habitat patches within the matrix can enhance amphibian dispersal, thereby increasing the ability of dispersing animals to inhabit or to recolonize a P&GS following local extinction.

Western red-back salamanders were responsible for 80% of Non-*Ensatina* captures. Non-*Ensatina* abundance was highest at sites with little fine woody debris, as were SCR and SCRE. Sticks, twigs and small branches constitute fine woody debris (0-10 cm diameter) and may represent inhospitable substrates and or physical barriers to that inhibited either amphibian capture or movement.

Conservation and Management Implications

Although P&GSs within the Greater Portland Metropolitan area appear to have already undergone faunal relaxation, it is nonetheless still important to consider the implications of my results for the persistence of the current amphibian communities. My findings suggest that the first consideration for the protection of the amphibian communities is to ensure that appropriate macrohabitat/patch features be maintained within P&GSs. To sustain the current species richness in P&GSs, efforts must be made to maintain the current area of larger P&GSs, while promoting the development of a complex tall shrub understory, beneath a diverse tree community. Additionally, maintaining the number and proximity of forest patches surrounding each P&GSs should be a priority. Conditions at the microenvironment scale tend to reflect the larger general forest structure within the macrohabitat/patch, thus the maintenance of a diverse forest canopy should also create microenvironmental conditions that would support large amphibian populations. Landscape context appears to play only a secondary, or even a minor role, for locally occurring woodland species since most do not undertake lengthy migrations. On the other hand, landscape composition and configuration may play a very critical role. Loss of connectivity may diminish the ability of these species to recolonize a site following local extinction. For those species that do seasonally migrate, landscape composition and configuration is particularly important to sustaining local populations in fragmented landscapes. The capacity to which these animals can traverse

inhospitable matrix determines the likelihood for their future persistence. The creation of uncommon habitats such as permanent ponds and stream restoration within P&GSs, combined with reintroduction, may also permit establishment of breeding populations of some species (rough skin newt, red-leg frog, long-toed salamander, northwestern salamander, and Pacific giant salamander) currently missing from otherwise suitable habitat. Finally the abundance of amphibians in all P&GSs was low compared to studies conducted within non-urbanized sites from the Northwest, and additional research is needed to determine if urban populations of amphibians typically exhibit low densities. If this is the case, small isolated populations such as these, which inherently have an increased likelihood of local extinction, may have a difficult time maintaining viable populations, without direct management intervention and protection

Table 1. Amphibian study sites with greenspace or park name and average patch characteristics. Site numbers coincide with numbers in Figure 1.

Site number	Park and Greenspace name	Area (h)	Elevation (m)	Shape	Proximity	Wetland density (m ² /ha)	Stream density (m ² /ha)	Potential relative radiation
1	Canal Acres	13.1	39.4	2.7	722	2082.4	39.4	16353
2	Forest Park South	1538.4	261.9	4.4	19670	0.9	261.9	14450.
3	Forest Park North	731.8	258.5	2.7	12996	0.0	258.5	15758
4	George Himes North	8.9	131.9	1.9	186	0.0	131.9	13819
5	Hyland Forest Park	11.7	103.7	1.4	1	878.9	103.7	15654
6	Keller Woodland	71.7	195.6	2.5	1146	0.0	195.6	14110
7	Lesser Park	18.3	171.6	4.5	491	0.0	171.6	16749
8	Lowami Hart Park	11.8	61.4	1.6	45	3356.6	61.4	15974
9	Maicara Park	11.0	158.3	1.8	130	0.0	158.3	16665
10	Marshall North	10.4	97.0	3.1	1223	0.0	97.0	16322
11	Mt Talbert	114.0	165.9	2.3	1292	38.2	165.9	16466
12	Powell Butte	129.0	134.6	3.5	170	0.0	134.6	17573

13	Riverview Cemetery	80.5	102.0	2.8	768	0.0	102.0	15928
14	Springbrook Park	23.0	123.5	2.2	25	11.8	123.5	16370
15	Tryon Creek Park	288.3	62.9	4.0	1368	0.0	62.9	16286
16	Tualatin Hills Park	72.0	57.0	2.4	43	1276.6	57.0	16474
17	West Portland Park	14.1	184.5	1.9	9	0.0	184.5	16912

Shape, measured by shape index, 1.0 = perfectly square and decreases as patches become less Euclidian (i.e. more edgy)

Proximity, measured by proximity index = the sum of patch *i* area divided by the square distances between patch *i* and the focal patch for all wooded areas in the landscape

Wetland density and stream density, calculated by dividing the total area of each variable by the total area (ha) of the patch, and then multiplying by 100.

Potential relative radiation, a GIS-based proxy variable estimating average relative solar radiation.

Table 2. Description of variables measured for microenvironmental conditions at P&GSSs, and the factor loadings generated by principal component analysis of (A) ground cover features, (B) physical features of the soil, and (C) coarse woody debris (logs and snags). Only loadings of 0.45 or better were considered for interpretation.

(A) GROUND COVER			
Variable and description	COVER1	COVER2	COVER3
Herb cover (%)			0.8361
Leaf cover (%)	0.456		
Moss cover (%)			
Cover of fine woody debris <2.54 (%)		-0.512	
Cover of fine woody debris >2.54 <10 cm (%)		-0.648	
Cover of bare soil (%)	-0.456		
Leaf litter depth (cm)	0.568		
Eigenvalue (% variation)	2.51 (35.9)	1.96 (28.1)	1.28 (18.4)

(B) PHYSICAL FEATURES OF SOIL

Variable and description	SOIL1	SOIL2
Soil moisture (%)*		0.665
Soil temperature (C)*		-0.583
Average site soil pH ([H ⁺])*	-0.611	
Minimum site soil pH ([H ⁺])*	-0.459	
Maximum site soil pH ([H ⁺])*	-0.587	
Eigenvalue (% variation)	2.44 (48.8)	1.32 (26.4)

(C) COARSE WOODY DEBRIS

Variable and description	CWD1	CWD2
Volume of logs/snags in decay class 1 (m ³) (=LGSNG1)		0.690
Volume of logs/snags in decay class 2 (m ³) (=LGSNG2)		0.585
Volume of logs/snags in decay class 3 (m ³) (=LGSNG3)		

Volume of logs/snags in decay class 4 (m ³) (=LGSNG4)	0.534
Volume of logs/snags in decay class 5 (m ³) (=LGSNG5)	0.511
Total volume of all logs/snags (m ³) (=LGSNGTV)	0.572
Eigenvalue (% variation)	2.57 (42.9)
	1.56 (25.9)

* Data used in PC analyses acquired from PFA locations only (n=47 survey plots)

Table 3. Description of patch variables used to characterize macrohabitat features of P&GSs, and the factor loadings generated by the principal components analysis variables at both scales. Only variables with loadings of 0.45 or better were used for interpretation of axes

MACROHABITAT	Variable and description	MACROHAB1	MACROHAB2	MACROHAB3	MACROHAB4
	Shrub density, 0.0-0.5 m (avg. # of hits)			0.815	
	Shrub density, 0.5-1.0 m (avg. # of hits)			0.503	
	Shrub density, 1.0-1.5 m (avg. # of hits)				
	Shrub density, 1.5-2.0 m (avg. # of hits)				
	Shrub density, 2.0-2.5 m (avg. # of hits)	0.477			
	Shrub density, 2.5-3.0 m (avg. # of hits)				
	Importance value (IV) of conifers (0-100)				0.464
	IV of angiosperms (0-100)				-0.464
	Canopy closure (%)		0.535		
	Eigenvalue (% variation)	3.57 (39.7)	1.91 (21.3)	1.31 (14.6)	1.07 (11.9)

Table 4. Correlation coefficients from Pearson correlation ($p = 0.05$) of landscape variables with landscape principal components acquired from 48 sites, which include the 17 amphibian sites.

LANDSCAPE	Variables and description		
	LAND1	LAND2	LAND3
Cover of forest in 1 km buffer (%)	-0.7277	-0.5056	
Mean proximity of all forest patches in 1 km buffer (%)	-0.9466		
Cover of built forest in 1 km buffer (%)		-0.9115	
Cover of commercial/ industrial in 1 km buffer (%)		0.5177	0.7404
Cover of treeless open space in 1 km buffer (%)		0.8557	
Cover of single-family residential in 1 km buffer (%)	0.9072		-0.5648
Cover of multi-family residential in 1 km buffer (%)		0.5322	
Cover of single and multifamily residential in 1 km buffer (%)	0.9534		-0.5350
Building density in 1 km buffer (parcels/ha)	0.9681		
Population density in 1 km buffer (people/ha)	0.9534		
Street density in 1 km buffer (streets/ha)			

Table 5. Summarization of variables used in the hierarchical partial regressions of amphibian species richness and capture rates. With the exception of biogeographic features, all variables are axes derived from principal components analyses and represent composite descriptions of major gradients of variation at that level.

(A) Microenvironmental	Description
COVER1	Contrast of increasing bare soil (-) with leaf cover and litter depth (+)
COVER2	Gradient of increasing cover SFWD and LFWD (+) (FWD = SFWD and LFWD)
COVER3	Gradient of increasing herb cover (+)
SOIL1	Gradient of declining pH (+) (positive scores have lower pH)
SOIL2	Contrast of sites with dry warm soils (-) with sites with cooler moister soils (+)
CWD1	Gradient of increasing LGSNG4, LGSNG5, LGSNGTV (+)
CWD2	Gradient of inclining LGSNG1, LGSNG2 (+)
(B) Macrohabitat/patch	Description
MACROHAB1	Gradient of increasing density of high shrub (+)

MACROHAB2	Gradient of increasing forest canopy cover (+)
MACROHAB3	Gradient of increasing (+) low shrub density
MACROHAB4	Contrast of high IV of angiosperms (-) with high IV of conifers (+)
ELEVATION	Park or greenspace elevation (m)
SLOPE	Park or greenspace slope (°)
PRR	Park or greenspace potential relative solar radiation
AREA*	Park or greenspace area (ha)
WETLAND*	Park or greenspace wetland density (m ² /ha)
STREAM*	Park or greenspace stream density (m ² /ha)
PROXIMITY*	Sum of patch <i>i</i> area divided by the square distances between patch <i>i</i> and the focal patch for all wooded areas in the 1000 m buffer
SHAPE	1.0 = perfectly square and increases as patches become less Euclidian (i.e. more edgy)

(C) LANDSCAPE

Description

LAND1	Contrast of increasing proximity of forest patches and high forest cover in buffer (-) with increasing building, population, and residential density (+)
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LAND2

Contrast of large amounts of built forest (-) with areas with a high proportion of the buffer zoned as open space (+)

LAND3

Contrast of increasing residential land use (-) with COM/IND land use (+)

* Kolmogorov-Smirnov test for normality $P < 0.05$; log-transformed before use.

Table 6. Mean amphibian detection probabilities from PFA sampling when species were detected at least once at a site during field sampling 2002-2003

Field Season	<i>E. eschscholtzi</i>	<i>P. vehiculum</i>	<i>T. granulosa</i>	<i>R. aurora</i>	<i>A. macrodactylum</i>	<i>A. gracile</i>	<i>H. regilla</i>	<i>D. tenebrosus</i>	<i>R. catesbeiana</i>
Fall 2002	0.54	0.50	0.50	0.50	0.67	0.33	0.00	0.00	0.00
Spring 2003	0.32	0.00	0.50	0.25	0.00	0.00	0.00	0.33	0.00
Fall 2003	0.22	0.25	0.50	0.29	0.29	0.07	0.07	0.07	0.07
Fall 2002, Fall 2003	0.38	0.37	0.50	0.39	0.48	0.20	0.04	0.04	0.04
All field seasons	0.36	0.25	0.50	0.35	0.32	0.13	0.02	0.13	0.02

Table 7. Total amphibian species richness all methods TSR from PFA sampling and all additional methods for 2003-2004 field seasons.

Site	<i>E. eschscholtzi</i>	<i>P. vehiculum</i>	<i>T. granulosa</i>	<i>R. aurora</i>	<i>A. macrodactylum</i>	<i>A. gracile</i>	<i>H. regilla</i>	<i>D. tenebrosus</i>	<i>P. dumni</i>	<i>R. catesbeiana</i>	Total species
1	X _p			X _a	X _p		X _a				4
2	X _p	X _p									2
3	X _p	X _a		X _a			X _a		X _a		6
4	X _p	X _p									2
5	X _p						X _a				2
6	X _p	X _a							X _a		3
7	X _p										2
8	X _p	X _a					X _a				2
9	X _p						X _a				4
10	X _p	X _p									1
11	X _p	X _p	X _p				X _a				3
12	X _p			X _a			X _a				5
					X _p						4

Table 8. Correlation coefficients between microenvironment, macrohabitat/patch, and landscape variables with a $r \geq 0.577$.

	<u>LAND1</u>		<u>AREA</u>
PROXIMITY	-0.825	LAND1	-0.831
MACROHA3	-0.608	PROXIMITY	0.644
SOIL2	-0.665	STREAM	0.739
COVER1	-0.587		
	<u>SLOPE</u>		<u>CWD2</u>
STREAMD	0.673	COVER1	0.596
WETLAND	-0.602	SOIL1	-0.596
	<u>MACROHAB2</u>		<u>LAND2</u>
CWD1	-0.588	COVER2	-0.690
	<u>PROXIMITY</u>		<u>MACROHAB1</u>
SHAPE	0.641	SOIL1	-0.712
	<u>MACROHAB4</u>		
WETLAND	-0.623		
ELEVATION	0.722		

FIGURE LEGEND

Figure 1. Map of amphibian study sites of the greater metropolitan area of Portland Oregon

Figure 2. (A) Regression of park and greenspaces area with amphibian species richness.

(B) Regression of park and greenspace proximity to other forest fragments in 100 m buffer with amphibian species richness

Figure 3. Maximally packed amphibian presence/absence (arranged in columns) matrix for 17 parks and greenspaces (arranged in rows) of the Portland Metropolitan area.

Figure 4. Results of partial regression for total species richness using all 17 parks and greenspaces.

Figure 1. Map of amphibian study sites of the greater metropolitan area of Portland Oregon

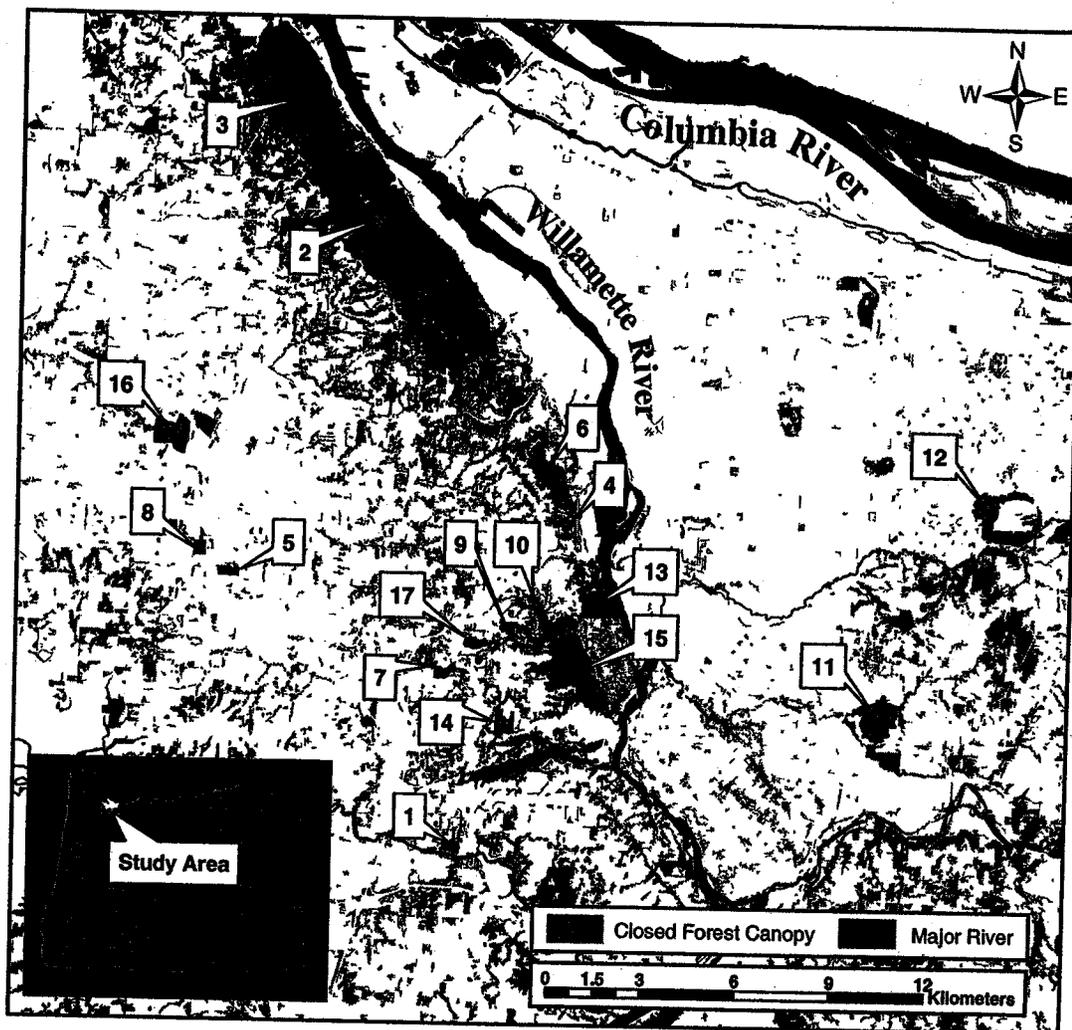


Figure 2. (A) Regression of park and greenspaces area with amphibian species richness. (B) Regression of park and greenspace proximity to other forest fragments in 100 m buffer with amphibian species richness

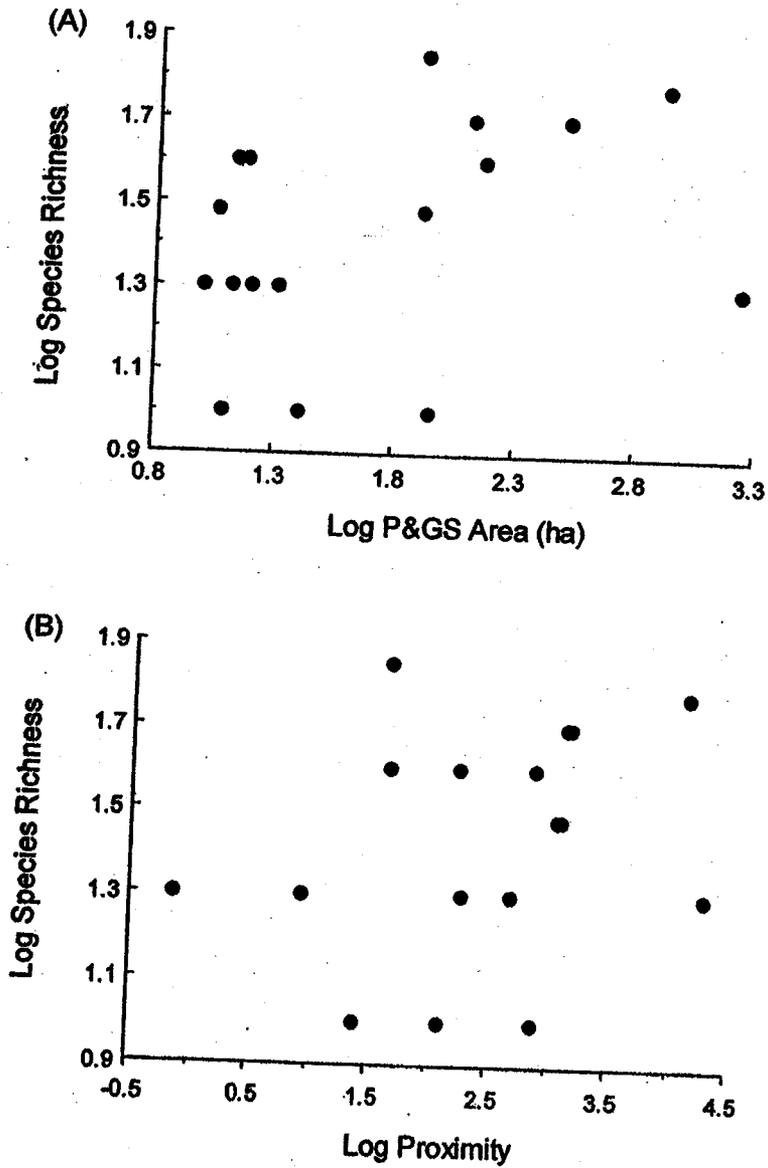


Figure 3. Maximally packed amphibian presence/absence (arranged in columns) matrix for 17 parks and greenspaces (arranged in rows) of the Portland Metropolitan area.

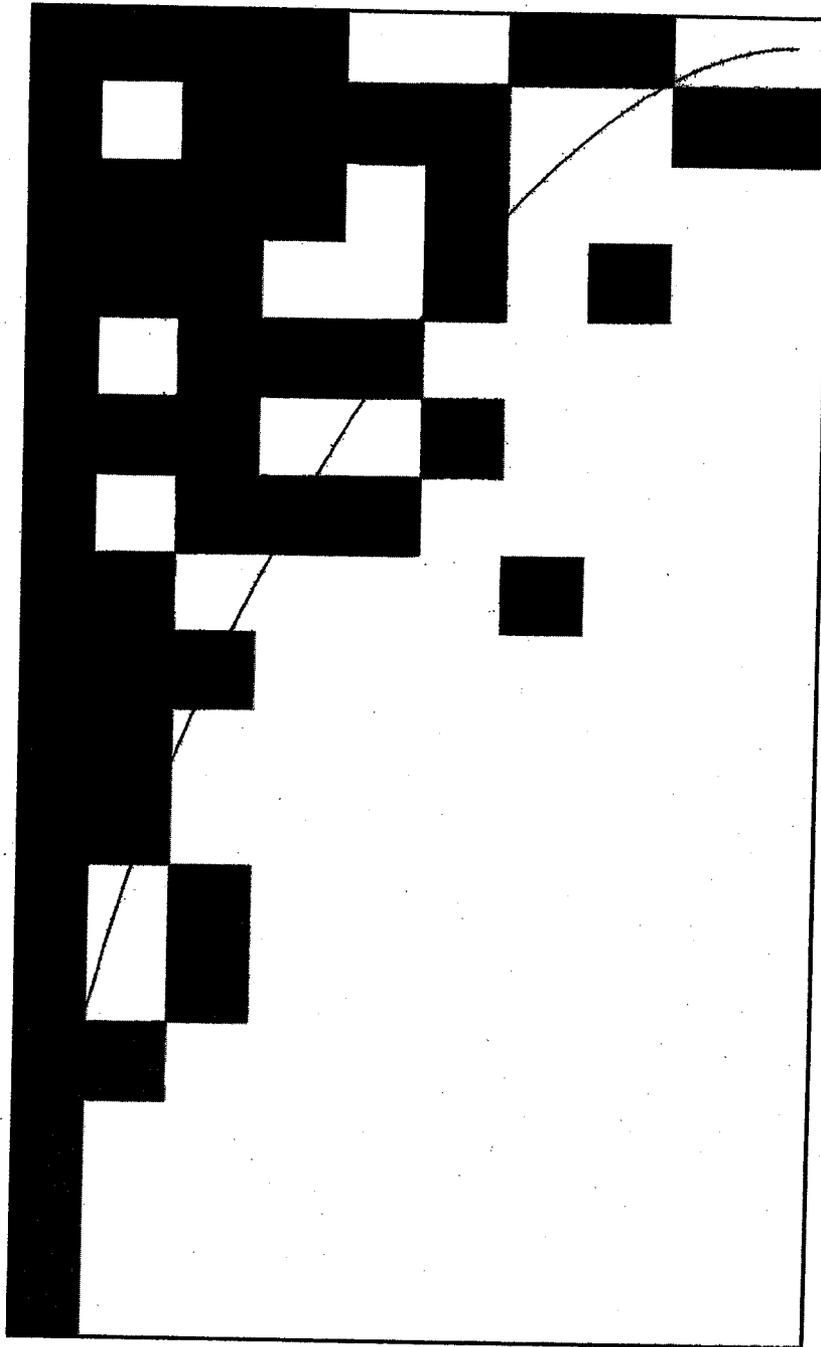
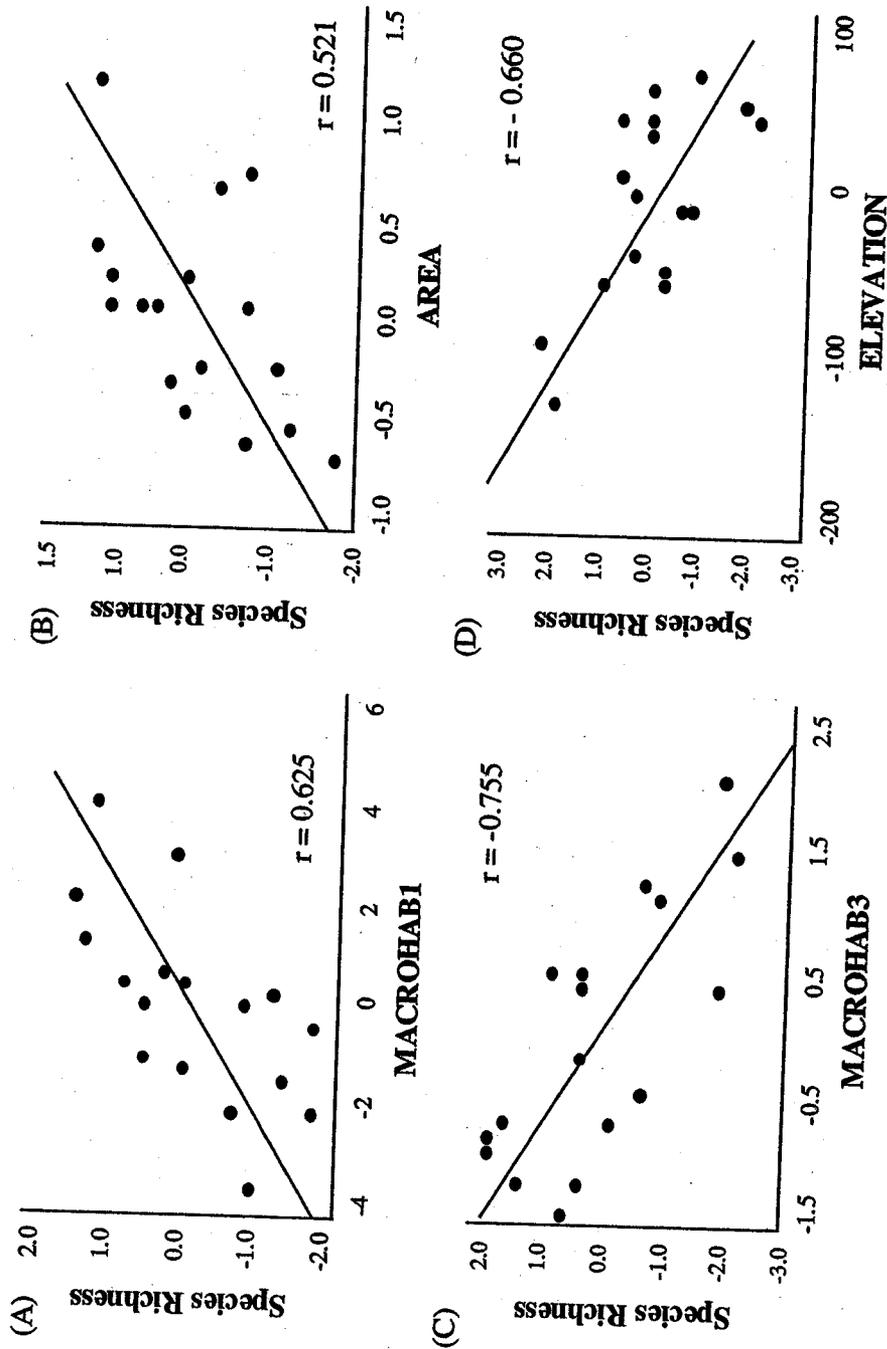


Figure 4. Results of partial regression for total species richness using all 17 parks and greenspaces.



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Appendix A

Amphibian captures from PFA's comparing fall 2002 to fall 2003 with number of (1) captures:trap nights fall 2002 (2.)

captures:trapnights fall 2003 (3) number of detections:number of trapping sessions fall 2002, (4) number of detections:number of trapping sessions fall 2003

Site	<i>E. eschscholtzi</i>	<i>P. vehiculum</i>	<i>T. granulosa</i>	<i>R. aurora</i>	<i>A. macrodactylum</i>	<i>A. gracile</i>	<i>H. regilla</i>	<i>D. tenebrosus</i>	<i>R. catesbeiana</i>
1	1. (1:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)
	2. (2:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)	2. (1:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)
	3. (1:3)	3. (0:3)	3. (0:3)	3. (0:3)	3. (0:3)	3. (0:3)	3. (0:3)	3. (0:3)	3. (0:3)
	4. (1:12)	4. (0:12)	4. (0:12)	4. (0:12)	4. (1:12)	4. (0:12)	4. (0:12)	4. (0:12)	4. (0:12)
2	1. (4:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)
	2. (3:1296)	2. (1:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)	2. (0:1296)
	3. (4:4)	3. (0:4)	3. (0:4)	3. (0:4)	3. (0:4)	3. (0:4)	3. (0:4)	3. (0:4)	3. (0:4)
	4. (3:12)	4. (1:12)	4. (0:12)	4. (0:12)	4. (0:12)	4. (0:12)	4. (0:12)	4. (0:12)	4. (0:12)
3	1. (10:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)	1. (0:144)

2. (5:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296)
 3. (2:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
 4. (3:12) 4. (0:12) 4. (0:12) 4. (0:12) 4. (0:12) 4. (0:12) 4. (0:12) 4. (0:12)

4 1. (6:72) 1. (8:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
 2. (2:864) 2. (6:864) 2. (0:864) 2. (0:864) 2. (0:864) 2. (0:864) 2. (0:864) 2. (0:864)
 3. (2:4) 3. (3:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
 4. (2:14) 4. (5:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14)

5 1. (4:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
 2. (6:860) 2. (0:860) 2. (0:860) 2. (0:860) 2. (0:860) 2. (0:860) 2. (0:860) 2. (0:860)
 3. (2:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3)
 4. (4:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14)

6 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
 2. (4:880) 2. (0:880) 2. (0:880) 2. (0:880) 2. (0:880) 2. (0:880) 2. (0:880) 2. (0:880)
 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3)
 4. (2:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14)

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- 1. (5:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96)
 - 2. (4:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236)
 - 3. (2:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
 - 4. (3:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14)
- 8
- 1. (4:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
 - 2. (2:1320) 2. (0:1320) 2. (0:1320) 2. (0:1320) 2. (0:1320) 2. (0:1320) 2. (0:1320) 2. (0:1320)
 - 3. (2:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3)
 - 4. (2:15) 4. (0:15) 4. (0:15) 4. (0:15) 4. (0:15) 4. (0:15) 4. (0:15) 4. (0:15)
- 9
- 1. (4:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96)
 - 2. (1:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236)
 - 3. (2:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
 - 4. (1:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14)
- 10
- 1. (11:72) 1. (10:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
 - 2. (6:840) 2. (9:840) 2. (0:840) 2. (0:840) 2. (0:840) 2. (0:840) 2. (0:840) 2. (0:840)
 - 3. (3:3) 3. (2:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3)

4. (5:15) 4. (0:15) 4. (5:15) 4. (0:15) 4. (0:15) 4. (0:15) 4. (0:15) 4. (0:15)
- 11 1. (1:72) 1. (1:72) 1. (1:72) 1. (1:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
2. (1:948) 2. (0:948) 2. (1:948) 2. (0:948) 2. (0:948) 2. (0:948) 2. (0:948) 2. (0:948) 2. (0:948)
3. (1:3) 3. (1:3) 3. (1:3) 3. (1:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3) 3. (0:3)
4. (1:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (0:11)
- 12 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72) 1. (0:72)
2. (2:808) 2. (0:808) 2. (0:808) 2. (0:808) 2. (3:808) 2. (0:808) 2. (0:808) 2. (0:808) 2. (0:808)
3. (0::3) 3. (0::3) 3. (0::3) 3. (0::3) 3. (0::3) 3. (0::3) 3. (0::3) 3. (0::3) 3. (0::3)
4. (2:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (3:11) 4. (0:11) 4. (0:11) 4. (0:11) 4. (0:11)
- 13 1. (3:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96)
2. (5:1248) 2. (0:1248) 2. (0:1248) 2. (0:1248) 2. (0:1248) 2. (0:1248) 2. (0:1248) 2. (0:1248) 2. (0:1248)
3. (2:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
4. (4:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14) 4. (0:14)
- 14 1. (5:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96)

- 2. (9:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296) 2. (0:1296)
 - 3. (2:14) 3. (0:14) 3. (0:14) 3. (0:14) 3. (0:14) 3. (0:14) 3. (0:14) 3. (0:14)
 - 4. (6:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13)
- 15
- 1. (2:133) 1. (1:133) 1. (0:133) 1. (0:133) 1. (0:133) 1. (0:133) 1. (0:133) 1. (0:133)
 - 2. (9:1664) 2. (5:1664) 2. (2:1664) 2. (0:1664) 2. (0:1664) 2. (1:1664) 2. (0:1664) 2. (0:1664)
 - 3. (1:4) 3. (1:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
 - 4. (5:14) 4. (3:14) 4. (2:14) 4. (0:14) 4. (0:14) 4. (1:14) 4. (0:14) 4. (0:14)
- 16
- 1. (1:72) 1. (0:72) 1. (31:72) 1. (2:72) 1. (1:72) 1. (0:72) 1. (0:72) 1. (0:72)
 - 2. (2:1320) 2. (0:1320) 2. (38:1320) 2. (5:1320) 2. (12:1320) 2. (1:1320) 2. (0:1320) 2. (1:1320)
 - 3. (1:3) 3. (0:3) 3. (2:3) 3. (2:3) 3. (2:3) 3. (1:3) 3. (0:3) 3. (0:3)
 - 4. (2:14) 4. (0:14) 4. (12:14) 4. (4:14) 4. (7:14) 4. (1:14) 4. (0:14) 4. (1:14)
- 17
- 1. (4:96) 1. (3:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96) 1. (0:96)
 - 2. (4:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236) 2. (0:1236)
 - 3. (2:4) 3. (2:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4) 3. (0:4)
 - 4. (3:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13) 4. (0:13)

Appendix B

Amphibian captures from PFA for spring 2003 with number of (1) captures:trap nights (2) number of detections:number of trapping

sessions

Site	<i>E. eschscholtzi</i>	<i>P. vehiculum</i>	<i>T. granulosa</i>	<i>R. aurora</i>	<i>A. macrodactylum</i>	<i>A. gracile</i>	<i>H. regilla</i>	<i>D. tenebrosus</i>	<i>R. catesbeiana</i>
1	1. (5:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)
	2. (2:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
2	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)
	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)
3	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)	1. (0:108)
	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)
4	1. (1:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (1:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
5	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)

	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
6	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
7	1. (1:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (1:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)
8	1. (1:132)	1. (0:132)	1. (1:132)	1. (0:132)	1. (0:132)	1. (0:132)	1. (0:132)	1. (0:132)	1. (0:132)
	2. (1:4)	2. (0:4)	2. (1:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
9	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)
10	1. (1:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
11	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)	1. (0:72)
	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)

12	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
13	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)
14	1. (0:84)	1. (0:84)	1. (0:84)	1. (0:84)	1. (0:84)	1. (0:84)	1. (0:84)	1. (0:84)	1. (0:84)
	2. (1:3)	2. (1:3)	2. (1:3)	2. (1:3)	2. (1:3)	2. (1:3)	2. (1:3)	2. (1:3)	2. (1:3)
15	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)
	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)
16	1. (0:120)	1. (0:120)	1. (6:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)	1. (0:120)
	2. (0:4)	2. (0:4)	2. (3:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)	2. (0:4)
17	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)	1. (0:96)
	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)	2. (0:3)

