

BIOGEOGRAPHY OF VASCULAR PLANTS AND SMALL MAMMALS IN  
FOREST FRAGMENTS IN PORTLAND, OREGON: EFFECTS OF LOCAL  
HABITAT, LANDSCAPE COMPOSITION AND PATCH SIZE

by

NATHANAEL ISSAC LICHTI

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

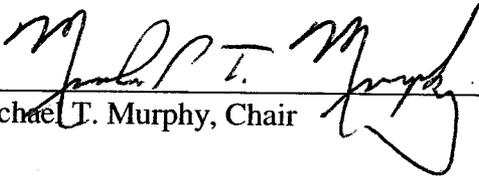
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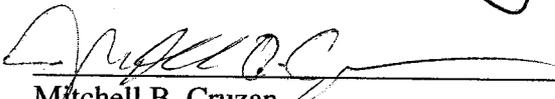
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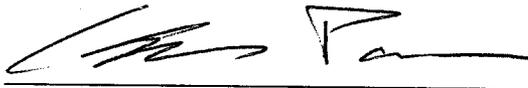
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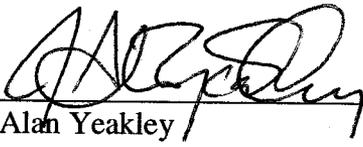
The abstract and thesis of Nathanael Issac Lichti for the Master of Science in Biology were presented July 31, 2004, and accepted by the thesis committee and the department.

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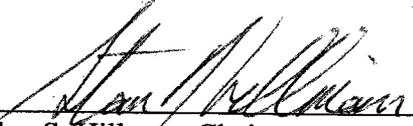
  
\_\_\_\_\_  
Michael T. Murphy, Chair

  
\_\_\_\_\_  
Mitchell B. Cruzan

  
\_\_\_\_\_  
Yangdong Pan

  
\_\_\_\_\_  
J. Alan Yeakley  
Representative of the Office of Graduate Studies

DEPARTMENT APPROVAL:

  
\_\_\_\_\_  
Stanley S. Hillman, Chair  
Department of Biology

## ABSTRACT

An abstract of the thesis of Nathanael Issac Lichti for the Master of Science in Biology presented July 30, 2004.

Title: Biogeography of Vascular Plants and Small Mammals in Forest Fragments in  
Portland, Oregon: Effects of Local Habitat, Landscape Composition and Patch  
Size

Urban development is a major contributor to habitat loss and fragmentation in North America, and results in the degradation of habitat remnants within cities through trampling, microclimatic alteration, and exotic species invasion. Such changes may reduce the suitability of urban forest remnants for wildlife, resulting in the systematic exclusion of many species from small, isolated, or edge-heavy sites. To determine the effects of landscape fragmentation by urbanization on Pacific Northwest forest communities, I surveyed the structure and floristic composition of 48 forest fragments in the greater Portland, Oregon metropolitan area, and live-trapped small mammals at a subset of 25 of these sites. I used multiple regression, in combination with ordinations and nested subset analyses, to compare species richness, diversity, and

composition with a suite of environmental parameters including local habitat structure, site topography, water availability, patch size, shape, and isolation, landscape composition around fragments, and human disturbance. The results demonstrated that smaller, more isolated forest fragments in more urbanized landscapes were structurally and floristically simplified and degraded. Early-seral, disturbance-tolerant tree species and invasive, non-native shrubs dominated such parks, which were also deficient in coarse woody debris and lacked developed organic litter layers. Small mammals lost richness in patches with fewer wetlands and streams, and in smaller, more isolated, more degraded fragments. The latter also contained more non-native species. Changes in the physical structure and plant composition of small, urbanized forest fragments may have combined with patch isolation by urban development to reduce small mammal richness. Retention of canopy trees in the developed urban landscape mitigated these effects to some extent, possibly by attenuating microclimatic edge effects and providing movement corridors for a variety of small mammals, especially squirrels. However, canopy cover in the developed matrix was also associated with shade-tolerant invasive plants, such as English ivy (*Hedera helix*). Overall, these results demonstrate that urban refuges should be viewed in a context that accounts for species use of the surrounding landscape, as well as local habitat conditions.

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In memory of Richard B. Forbes,  
who first introduced me to the mammals of Oregon.  
Although I knew him only a short time, his love of nature  
and dedication to teaching are a continuing inspiration.

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## CHAPTER 1: OVERVIEW AND GENERAL BACKGROUND

Forests in the Pacific Northwest are changing. This is especially true west of the Cascade Range, where much of the centuries-old Douglas-fir (*Pseudotsuga menziesii*) forest that once blanketed higher elevations has been converted to younger, managed stands that are cut on 60 – 80 year rotations (Harris 1984). Consequently, most of the research on forest ecology that has taken place in the region has focused on timber management and its effects. Like rural areas and wildlands everywhere, forests in western Oregon and Washington are also facing increasing pressure from human population growth and urban development (Alig *et al.* 2004, Baker *et al.* 2004, Butler *et al.* 2004). Although urbanization, like timber harvest, results in the reduction and fragmentation of forests at the landscape level, it is a fundamentally different disturbance with regard to its spatial pattern, temporal scale, and effects on ecological processes (Pickett *et al.* 2001). This thesis investigates the consequences of forest fragmentation by urban development by examining the biogeographic variation in plant and small mammal communities in patches of semi-natural, second-growth forest in the greater Portland, Oregon metropolitan area.

The choice of these particular groups of organisms is not accidental. Forest vegetation, and trees in particular, provide fundamental and critical habitat functions for small mammals, including foraging, nesting sites, cover and shelter from predators, and maintenance of habitable microclimates. Many Northwestern mammals achieve

their highest densities in mature, diverse conifer forests containing large trees and their associated understory plants (Verts and Carraway 1998). In addition, most of these functions are not limited to living plants. Organic litter created by decaying vegetation provides cover for numerous small insectivore, and coarse woody debris, especially downed logs, provides shelter, favorable microclimates, nesting sites, and food in the form of insects and fungi, and continues to contribute to small mammal population throughout the decay process (reviewed by Verts and Carraway 1998, Hallett *et al.* 2003, McComb 2003). Several northwestern mammals also rely heavily on the hypogeous ectomycorrhizal fungi that exist as symbiotes of all coniferous trees (Verts and Carraway 1998, Hallett *et al.* 2003, Luoma *et al.* 2003, Smith *et al.* 2003). The sporocarps of these fungi are eaten by most rodents and insectivores, and they serve as the primary food for both western red-backed voles (*Clethrionomys californicus*) and northern flying squirrels (*Glaucomys sabrinus*) (Maser *et al.* 1985, Hayes *et al.* 1986).

Small mammals are also prodigious ecosystem engineers, and play a fundamental role in creating and maintaining the forest plant communities upon which they and other vertebrates depend. Mammalian mycophagy provides the primary mode of spore dispersal for ectomycorrhizae, which conifers require for establishment and growth (Aubry *et al.* 2003, Luoma *et al.* 2003). Seed predation by granivorous rodents can result in the reduction or even complete removal of cone or seed crops of both conifers (reviewed by Aubry *et al.* 2003, Hallett *et al.* 2003) and herbs (e.g. Tallmon *et al.* 2003). However, caching behavior, particularly by squirrels (e.g.

*Tamiasciurus douglasii*) and chipmunks (e.g. *Tamias townsendii*), may also assist in the dispersal of these seeds (Aubry *et al.* 2003). Based on results from drier, less complex pine forests, conifer seeds in caches may germinate more frequently than uncached seeds (VanderWall 1992, Hallett *et al.* 2003). Arboreal rodents also clip the terminal buds of live conifers, leading to the creation of platforms which may be used for nest construction by raptors and other vertebrates (Aubry *et al.* 2003). In addition to these impacts on vegetation, small mammals impact other vertebrate populations directly through nest predation (e.g. Fenske-Crawford and Niemi 1997) and form the prey base for many carnivores, raptors, and owls.

The remainder of my thesis is divided into three chapters. The next chapter describes and analyzes variation in the structure and composition of forest plant communities, and trees in particular, in relation to traditional island biogeographic variables such as patch size and isolation. Variation in relation to the land use composition of the developed matrix separating forest patches is also considered. The chapter concludes that smaller, more urbanized forest fragments contain simplified, degraded plant communities, and lays out several hypothetical mechanisms that may have contributed to this pattern. It also notes that the retention of an intact canopy in the matrix may benefit forest fragments isolated by urbanization. The third chapter examines the richness and composition of small mammal communities in relation to local habitat variation, landscape composition, and patch characteristics (e.g. area, isolation), and concludes that communities in Portland forest fragments are largely impoverished. This appears to be the result primarily of habitat degradation, but also

of fragment isolation by urban development. The final chapter summarizes the results of the first two chapters from a management perspective and lays out suggestions for future research on urban forest ecology in Portland.

CHAPTER 2: COMPOSITION AND STRUCTURE OF FOREST FRAGMENTS  
ISOLATED BY URBANIZATION IN PORTLAND, OREGON

**Abstract**

Urban growth, the most rapidly expanding form of land conversion in North America, causes significant habitat fragmentation and biodiversity loss. Development not only reduces habitat area and isolates remnant fragments, but also leads to substantial edge effects that can seriously degrade local habitats and vegetative communities. We sampled plant communities at 279 survey points in 48 second-growth forest fragments in Portland Oregon, and used regressions and canonical correspondence analyses to evaluate the effects of patch size and shape, landscape composition, underlying geophysical structure, and intensity of human use on species richness and composition, and forest structure. After correcting for spatial variation, the diversity of native woody species increased with patch area and declined with more complex patch shapes. Non-native richness and diversity declined with area, and increased in patches with complex shapes. The richness and diversity of non-native herbs also decreased with patch area. Native herbs increased with topographic complexity and declined with increased commercial or industrial land use in the surrounding landscape. Ordinations indicated that as the landscape became more urban and patch size declined, fragments lost late-successional and shade-tolerant species and became increasingly dominated by regionally common, early-seral trees.

This had the effect of homogenizing and simplifying forests, both compositionally and structurally. Smaller, more urban sites were also more vulnerable to invasion by non-native species. In addition, landscape composition influenced communities in a manner suggesting that retention of canopy tree cover around patches may have buffered microclimatic edge effects. However, it may have also facilitated invasion by shade-tolerant non-native plants.

### **Introduction**

Forest cover over much of the world has declined tremendously over the past century due to timber harvest, agricultural conversion, and urbanization. For example, forests in Oregon's urbanized Willamette River valley have declined 61.1% since 1972, and currently comprise only 12.1% of the landscape (American Forests 2001). This pattern is typical of much of North America, where urban development is a major contributor to forest loss and fragmentation (Butler *et al.* 2004). With the U.S. population projected to grow by 50% over the next half century (Hollmann *et al.* 2000), it is essential for ecologists and managers to understand how patterns of biotic diversity differ between urban forest patches and other fragmented systems (Moran 1984, Godefroid and Koedam 2003).

Historically most studies of fragmented biotic communities have worked within the context of island biogeographic or metapopulation models (Fahrig and Merriam 1994, Collinge 1996, Jules and Shahani 2003). These theories focus on different aspects of fragmentation ecology, but both emphasize the importance of patch area

and isolation in determining community composition (McArthur and Wilson 1967, Hanski 1999). Smaller patches are expected to support fewer individuals and fewer microhabitats. This increases the vulnerability of local populations to extinction through stochastic demographic processes and raises the likelihood that species' habitat requirements will not be met. As a result, smaller fragments contain fewer species. At the same time, increased patch isolation limits opportunities for recolonization from nearby populations.

Recently, the composition of the matrix separating patches has attracted increased theoretical and empirical attention (e.g. Gascon *et al.* 1999a, Ricketts 2001, Jules and Shahani 2003, Gardner and Gustafson 2004). The matrix's most obvious influence on vegetative communities arises from edge effects, which often dominate conditions in small, linear, or highly convoluted patches (Murcia 1995, Collinge 1996). In fragments surrounded by clear cuts or agricultural fields, higher light intensities at forest edges raise temperatures, reduce moisture (Chen *et al.* 1995), and increase shrub and herb densities (Ranney *et al.* 1981, Matlack 1994). Increased light also stimulates growth of some tree species (Chen *et al.* 1992). Community composition may change as fast growing competitors replace shade tolerant species (Metzger 2000), more xeric species take advantage of decreased soil moisture (Ranney *et al.* 1981), and exotic species invade from the surrounding matrix (Brothers and Spingarn 1992). In addition, tree mortality typically increases at forest edges (Chen *et al.* 1992, Esseen 1994).

Many anthropogenic disturbances also have higher impacts on edges (Matlack 1993). Trampling and stem breakage are common in heavily visited woods, and cause decreased recruitment and lower stem densities. This provides competitive advantages to species that regenerate quickly or colonize recently disturbed areas more rapidly (Littlemore and Barker 2001, Malmivaara *et al.* 2002). Soil compaction along trails stunts root growth in forest herbs and shrubs (Bhujju and Ohsawa 1998), and may provide invading species with routes into fragment interiors, similar to roads at landscape scales (Tyser and Worley 1992, Forman and Alexander 1998, Parendes and Jones 2000). Physiognomy, species diversity, and composition may also respond to dumping, wood cutting, excavation, and fire suppression, all of which vary with proximity to human dwellings (Matlack 1993, Collinge 1996).

The matrix is also the primary source of exotic invasions. Cities support a much higher diversity of plant species than do the surrounding ecosystems, but most of the plants in gardens, yards, and other managed landscapes are non-native (Hope *et al.* 2003, Zerbe *et al.* 2003). As a result, forests in residential communities may contain more exotics than those in agricultural landscapes (Moran 1984). Heterogeneity in the developed matrix may also cause differences among patches. For example, South American forest fragments adjacent to affluent neighborhoods held a higher proportion of exotics than those in poorer sections of the city, presumably as a result of more intensive landscaping (de la Maza *et al.* 2002). The composition of the matrix might also contribute to secondary effects by altering the behavior of pollinators, seed dispersers, and herbivores (e.g. Ricketts 2001, Tallmon *et al.* 2003).

In this report we use surveys of plant communities from remnant forest fragments in Portland, Oregon to test the hypotheses that patch size, shape, and isolation, in conjunction with the composition of the matrix, affected urban forest plant species diversity, composition, and structure. Partial multiple regression and partial canonical correspondence analysis were used to model environmental effects while controlling for broad spatial patterns. We predicted that small, isolated patches with complex shapes, and patches occupying more fragmented, urban landscapes would contain fewer native plant species, and greater proportions of disturbance-tolerant, matrix-associated, and non-native species. We also expected that these fragments would reflect earlier successional stages.

## **Methods**

### *Study location*

We sampled the vegetation in 48 second growth forest fragments (also referred to as patches or sites) located in the northern Willamette, Sandy, and lower Columbia River watersheds in the greater Portland, Oregon metropolitan area (approximately 45°31' N, 122°40' W; Fig. 1). Geologically, this region is characterized by broad alluvial flats punctuated by scattered volcanic buttes (Franklin and Dyrness 1973). It rises to low hills in the west and is bordered by the Columbia River Gorge in the east. The region spans the interface between the Western Hemlock and Willamette Valley vegetation zones of Franklin and Dyrness (1973). Elevation ranges from approximately 20 m on the valley floor to 250 m at the crest of the Tualatin Mountains

on the region's western edge. Cool, wet winters and warm, dry summers characterize the regional climate, with a 30-year average annual temperature of 11.8° C, and average precipitation of 95.0 cm per year (Taylor and Hannan 1999). About half of annual precipitation occurs as rain from December to February. Later seral stages in this area contain many shade tolerant conifers, including western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), and western red cedar (*Thuja plicata*), but mixed conifer-hardwood stands are much more common. Douglas fir (*Pseudotsuga menziesii*) and big-leaf maple (*Acer macrophyllum*) dominate most canopies.

The Portland region has a long history of human habitation and landscape management. Before European settlement in the mid 1800s, burning by Native Americans maintained oak savannas and grasslands throughout much of the Willamette Valley (Boyd 1986). Subsequent logging, agricultural development, and urbanization removed much of the low elevation forest cover, although fire suppression has allowed conifers to colonize new locations on the valley floor (Baker *et al.* 2004). Currently, urban development is confined to the limits of the Portland Urban Growth Boundary (UGB), a state mandated border established in 1973 to protect farmland and forests from encroaching sprawl. With the exception of Oxbow Regional Park (Site 12), all of our study sites lie within this boundary (Fig. 2-1).

Tree canopy covers an estimated 31% of the Portland landscape (Newman 1997). However, a third of that area consists of Forest Park, a large (c. 2000 ha) forest preserve in the northwest hills (Fig. 2-1, sites 1 and 2). Most other remnant habitats in the city also occur at higher elevations. Forests in the west hills are generally more

densely packed and inter-connected, while the buttes in the east are more isolated by residential development.

Specific land use histories for our sites were unavailable for this analysis. However, most were logged within the past century, and have a history of livestock grazing. Presently, the larger sites serve as regional destinations for a variety of recreational activities, including hiking, mountain biking, and horseback riding. In contrast, smaller parks are used primarily by local residents. Although most of our study sites are designated as city parks, we emphasize that they are not parks in the usual sense. Rather, they are fragments of more-or-less natural forest, retained within the city to provide wildlife habitat, movement corridors, and forest-related recreation (Metro 2002).

#### *Vegetation surveys*

We sampled 23 sites in 2002 and 45 in 2003; 20 were sampled in both years (total  $n = 48$ ). Sites were delimited on the basis of roads, building development, large areas of open water, and other deviations from forested understory habitat (see *Landscape analysis*, below). We identified potential sites using ArcGIS (ESRI 1999) and Regional Land Information System (RLIS, Metro 2004) data describing tree canopy coverage (see *Landscape analysis* below), and then selected the final sites non-randomly to represent the full range of available patch sizes (0.3 to 1538 ha). The need to obtain land owner permission to enter some sites also constrained selection.

All sites consisted of multistory, second-growth, mixed deciduous-coniferous forest with >50% canopy closure.

We established 2 to 16 survey points in each fragment, with a total of 279 points across the city. To capture the greater variety of microhabitats present in larger fragments, the number of plots varied with patch size. Forty-seven of the plots were associated with established amphibian pitfall arrays (Roberts, unpublished). The remaining 232 plots were located randomly within fragments to  $\pm 10$  m using ArcGIS and Garmin 12XL GPS units with external antennae (Garmin International, Olathe, Kansas, USA).

We quantified floristic and structural attributes of forests at all 279 points using a 10 m radius circular plot. Within each plot, we identified the species and measured the diameter breast height (DBH) of all live stems with  $DBH \geq 2.5$  cm and snags with  $DBH \geq 10$  cm. In addition, we recorded the midpoint diameter of all logs  $\geq 10$  cm diameter and visually estimated the length to 1 m of all logs and snags. These were also assigned a decay class, as described in Table 2-1 (Cline *et al.* 1980, Sollins 1982). We recorded the number of stems bearing English ivy (*Hedera helix*) over a height of 3 m as an indicator of the prevalence of this invasive plant in the plot. Three meters was chosen as a cut-off because preliminary field visits indicated that the presence of ivy at this height generally accompanied substantial infestation of the lower trunk.

To survey the herb and shrub layer, we laid two transects across each circular plot in each of the cardinal directions, or at  $45^\circ$  angles to the northernmost pit, for pitfall-associated plots (see Roberts, unpublished, for descriptions of pitfall arrays).

At 2 m intervals along the transects, we recorded the density of shrub foliage in 6 half-meter vertical layers by counting stem and leaf hits on a 3 cm diameter pole ( $n = 21$  per plot). Shrubs included all woody, perennial species, as well as large, persistent ferns (most notably western sword fern, *Polystichum munitum*).

At each 2 m station, we also estimated the amount of horizontal cover in herbs, moss, rock, sticks and twigs, woody debris (2.5 – 10 cm diameter), leaf litter, and bare ground using line-intercept methods along a meter-stick divided into 10 cm increments and laid perpendicular to the transect. Classifications were allowed to overlap. For example, one 10 cm section of the ruler might contain herbs, moss, and rocks. We measured the depth of the litter layer at the center of the ruler. In addition, we visually estimated canopy cover in 10% increments by sighting vertically through a 3 cm diameter, 10 cm long plastic tube at each 2 m station. We recorded the taxa of plants contributing to shrub and herb estimates at each transect station. Finally, we estimated the distance from the center of the plot to the nearest trail (*DTRAIL*) as an indicator of current human disturbance.

In most cases, individuals were identified to species. Caryophyllaceae, Cyperaceae, Juncaceae, Poaceae and some members of Lamiaceae and Liliaceae were identified only to family, and several other groups were identified to genus (see Appendix B). Thus, true species richness may have been underestimated for plots where these taxa were common. For simplicity, we use the term species to refer to individual plant taxa throughout the remainder of this paper. A complete list of the taxa identified and their corresponding codes is available in Appendix B. In most

cases codes are composed of the first 2 letters of the generic name and specific epithet. Nomenclature follows (Pojar and MacKinnon 1994).

Table 2-1 summarizes the structural variables. After classifying trees by DBH, we summed the number of stems in each size class at each plot. The volume of coarse woody debris was calculated separately for logs and snags in each decay class, and then summed for each category. Scores for shrub densities, ground cover classes, litter depth, and canopy cover were averaged for the plot.

To quantify composition, we calculated modified importance values for each tree species at each plot by adding relative abundance and relative dominance, as calculated from DBH, and multiplying the result by 50. Importance therefore varied from 0 to 100 for each species at each plot. Relative frequencies for shrubs and herbs at each plot were calculated as the proportion (converted to percentages) of transect stations at which they occurred. Based on these results, taxonomic richness and Shannon's diversity indices ( $H' = -\sum P_i \log_{10} P_i$ ) were calculated for each plot and averaged to obtain values for each site. The measure that we refer to as 'richness' is actually the mean number of species per unit area (plot), or species density (sensu Whittaker *et al.* 2001). Both measures were calculated separately for native and exotic species.

#### *Site geomorphology*

With the exception of Oxbow Park, we estimated the elevation (*ELV*), slope (*SLP*), and aspect of each vegetation plot using a 2.0 m digital elevation model (DEM;

Metro Regional Services, *unpublished data*) and ArcGIS. This was done by creating a 10 m buffer around the plot's center point (UTM coordinates) and averaging the values over all of the DEM pixels that intersected the buffer. Aspect was subsequently transformed as  $ASPECT = \cosine(45 - \text{DEGREES}) + 1$  (Beers *et al.* 1966). This transformation converts a circular aspect measure to a linear variable ranging from 0.0 (southwestern face) to 2.0 (northeastern face). It provides a measure of slope exposure that is relevant to vegetation (Ohmann and Spies 1998). Two-meter DEM data were unavailable for Oxbow, so a 10 m DEM was used with 30 m buffers instead. Consequently, estimates for this park were somewhat less precise.

Values for elevation, slope, and aspect were averaged for each site. We calculated the range of elevations sampled at each site (*RGELV*) to provide an estimate of topographic relief, and the density of wetland habitats (wetland area divided by total area, in hectares; *WET*) and permanent streams (m/ha; *STRM*) in each fragment to provide estimates of water availability. These were calculated from survey data included in RLIS (see below).

### *Landscape analysis*

We used ArcGIS and FRAGSTATS (McGarigal and Marks 1995) to assess the size, shape, and geographical isolation of study sites, and the landscape composition around the sites. The data used in these analyses were derived from the RLIS database maintained by Portland's Metro Regional Services (Metro 2004). The database included geographic information system (GIS) layers describing taxlot-level land use,

streets, US Census data, hydrologic features, topography, and canopy cover throughout the region. Data on building area and building value were available for most tax parcels, and 2001 aerial photos were available for the entire metropolitan area at 3.05 m (10 ft) pixel resolution. Information on tree canopy cover was included as digitized from the aerial photos. A 1998 version of this layer was used in site selection; all subsequent analyses used the 2001 layer.

Using RLIS land use categories and canopy cover maps and hydrologic layers, we created a categorical land use map for a 1 km buffer around each site. The map differentiated forest (*FOR*), developed areas with canopy cover (*DCAN*), developed areas lacking trees (see below), agricultural fields (*AG*), other open spaces that lacked significant canopy (e.g. parks, vacant lots; *OPEN*), and open water (*WATER*). We assumed that any area with visible canopy cover on aerial photos constituted forested habitat, as long as the built area in the underlying taxlot was  $\leq 5\%$  of the total parcel area (building area divided by parcel area). We also assumed that paved, public roads designated patch edges. This combination best reflected our estimates of forest understory edge positions from field surveys. Locations where canopy cover overlaid parcels that contained  $> 5\%$  built area were classified as developed canopy. Such locations typically represented parks or residential yards containing large trees, and often occurred at the edges of forest patches. Open spaces (*OPEN*) were classified as public, rural, or vacant in RLIS land use records, and lacked visible canopy on aerial photos. Treeless built areas were subdivided into residential (*RES*) and commercial-industrial (*COM*) land uses on the basis of tax records, resulting in a total of 8

categories. A ninth category (*UNDEF*) was used for treeless locations that lacked land use information in RLIS.

The final habitat maps were rasterized with 5 m pixels. Using FRAGSTATS (McGarigal and Marks 1995), we calculated patch *AREA* and the proximity index (*PROX*) for each patch. *PROX* is defined as the distance to all other forest patches in the landscape, weighted by the size of those patches (Gustafson and Parker 1992). We also calculated the *SHAPE* index as the patch's perimeter divided by the minimum perimeter possible for a maximally compact patch of equal area (McGarigal and Marks 1995). Because FRAGSTATS uses square pixels, *SHAPE* equals 1.0 for perfectly square patches and increases as they become more complex. Unlike simple perimeter-to-area ratio, *SHAPE* is not necessarily correlated to *AREA* (McGarigal and Marks 1995).

To obtain measures of landscape composition around each site, we calculated the percentage of each of the 9 land use categories in the buffer. In addition, we calculated the mean proximity index of all forest patches in the buffer (*MNPROX*). This provided an estimate of landscape scale forest connectivity. We also used ArcGIS to estimate human population density (*POP*), building density (*BUILD*), and street density (*STRT*) in each buffer. Population density was estimated using 2000 U.S. Census block data contained in RLIS. Populations were assumed to be evenly distributed throughout census blocks, and density was averaged over the buffer by weighting each block by the area of its overlap with the buffer. Building density was estimated as the number of tax parcels in the buffer having a building value or

building area greater than zero, and street density was calculated as the total length of roads divided by the buffered area. In all cases except *MNPROX*, the site fragment itself was excluded from landscape calculations. Table 2-2 summarizes the codes and descriptions of all patch, landscape, and geologic variables.

### *Statistical analyses*

We used ANOSIM, a non-parametric, permutation-based procedure analogous to ANOVA, to ensure that the pitfall-associated plots were unbiased. ANOSIM compares two or more groups of multivariate samples on the basis of a dissimilarity matrix (Clarke 1993). We used Bray-Curtis distance and 999 new permutations, and found no significant difference between pitfall-associated and random plots (structure:  $R = -0.062$ ,  $P = 0.946$ ; composition:  $R = -0.062$ ,  $P = 0.961$ ). Averaged values for the structural, compositional, and geological variables therefore included all sample plots at each site. After averaging, environmental variables were screened for normality using a Kolmogorov-Smirnov goodness-of-fit test, and where necessary, log-transformed to remove skew (Zar 1999). The remaining analyses used whole forest fragments as the unit of analysis.

Environmental variables exhibited varying levels of covariation (Table 2-3). We therefore used principal components analysis (PCA) to reduce the number of environmental variables and remove multicollinearity among landscape and geologic datasets. However, because we were interested in evaluating the effects of geomorphology and landscape structure separately, separate analyses were performed

on the two sets of variables. This also produced more easily interpreted axes. Analyses were carried out on correlation matrices, and only variables that could be normalized were included (see footnote, Table 2-2). We used the broken stick method to evaluate the importance of higher level axes (Frontier 1976). Factor loadings for the first three axes of both PCAs are reported in Table 2-4.

Our study sites were spatially clustered. On several occasions, this led to overlap among their 1 km buffers. Although the exact landscape conditions experienced by any given site are unique, this overlap means that the sites cannot be considered strictly statistically independent. Rather, they are spatially autocorrelated. We used a trend surface analyses (TSA) to test for spatial patterns in the vegetation data (Borcard *et al.* 1992). To do this, we regressed each dependent variable against the terms of the complete third order polynomial of the sites' UTM coordinates, using a stepwise approach to remove terms that did not contribute significantly to the regression equation. This approach allowed us to account for both linear and nonlinear spatial patterns in the environmental data, including patchy or discontinuous gradients (Borcard *et al.* 1992). We then partialled out significant spatial covariables and evaluated the effects of environmental variables on species richness and diversity using stepwise regression (Borcard *et al.* 1992, Fortin and Gurevitch 2001). All regressions used  $\alpha = 0.10$  to enter the model and  $\alpha = 0.15$  to exit, and were run in SPSS 11.5 (SPSS 2002).

Partial canonical correspondence analysis (PCCA) was used to examine the effects of environmental variation on species composition and structure in more detail.

CCA arrays sites and species along theoretical axes that explain the maximum possible variation in species composition, with the constraint that the axes must represent linear combinations of the independent variables (ter Braak 1995). In PCCA, the ordination axes are based on the residual variation left over after controlling for the influence of covariables, such as spatial coordinates (ter Braak 1988). In the resulting diagrams, axes represent composite gradients of the independent variables. Arrows show the direction of steepest increase in individual independent variables, and the angles between arrows and axes indicate correlations between these elements. The arrows' lengths indicate their degree of variation in the graph. Species are visualized as points, and located at their optimal position along the gradients. Species that are close together occurred at similar locations, and those that occupy the diagram's periphery are generally less common than those at the center.

The ordinations followed a similar two-step procedure to the one outlined above for the multiple regressions. Significant spatial terms were identified by forward selection in CANOCO 4.5, using 999 random permutations and  $\alpha = 0.10$  to enter the model (ter Braak and Smilauer 2002). The spatial terms were then used as covariables, while environmental independent variables were selected using the same forward selection process. Because particularly rare species can distort ordination results, we included only species that occurred in at least 10% of the sites (ter Braak 1995). Structural variables were standardized to z-scores to remove the effects of different measurement scales (ter Braak 1995). Because CANOCO cannot implement

CCA with negative values in the dependent variables, we added a constant value (3.5) to all standardized structural variables.

## Results

### *Overall patterns of plant composition and richness*

We detected a total of 62 tree and shrub species, of which 53 were native and 9 were exotic. We also detected 76 species of herbs, including 58 natives and 18 exotics. Mean taxonomic richness varied from 6.7 to 14.0 species per plot for trees and shrubs, respectively, and from 0.0 to 11.5 species per plot for herbs. Mean Shannon diversity ranged from 0.66 to 0.97 and from 0.00 to 0.87 for woody and herbaceous species, respectively. Table 2-5 lists site means for these variables.

Douglas fir (*PSME*) and big-leaf maple (*ACMA*) dominated the overstory at most sites, with overall mean importance values of 29.5 and 26.6, respectively. However, Oregon ash (*Fraxinus latifolia*, *FRLA*) and western red cedar (*THPL*) made up the largest portion of the canopy in one site each, and five sites were dominated by red alder (*Alnus rubra*, *ALRU*). Among understory trees and shrubs, California hazelnut (*Corylus cornuta*, *COCO*) and vine maple (*Acer circinatum*, *ACCI*) were the most common species, with mean importance values of 8.2 and 5.2, respectively. Six other species also dominated in at least one site, including oceanspray (*Holodiscus discolor*, *HODI*), red elderberry (*Sambucus racemosa*, *SARA*), Pacific dogwood (*Cornus nuttallii*, *CONU*), and three non-natives: English holly (*Ilex aquifolium*, *ILAQ*), hedge laurel (*Prunus laurocerasus*, *PRLA*), and European hawthorn (*Crataegus spp.*, *CRSP*).

Western sword fern (*Polystichum munitum*, *POMU*) was the most common small shrub (< 1.5 m), with an average frequency of 30.2%. A non-native, English ivy (*HEHE*) had the second highest frequency (mean = 25.1%). Other common shrubs included trailing blackberry (*Rubus ursinus*, *RUUR*), Himalayan blackberry (*Rubus discolor*, *RUDI*, also non-native), Oregon grape (*Berberis nervosa*, *BENE*), and snowberry (*Symphoricarpos albus*, *SYAL*). Less common, but still occurring at over 50% of the sites were salal (*Gaultheria shallon*, *GASH*) and thimbleberry (*Rubus parviflorus*, *RUPA*).

The greatest variation among common species was observed in the herbs, in which 12 species dominated in at least one site. The most common species encountered were *Galium sp.* (*GASP*), *Hydrophyllum tenuipes* (*HYTE*), *Tellima grandiflora* (*TEGR*), Poaceae (*POAC*), *Vancouveria hexandra* (*VAHE*), *Trillium ovatum* (*TROV*), *Disporum hookeri* (*DIHO*), and Cyperaceae (*CYPE*). *H. tenuipes* was the most common herb species overall, with an average frequency of 13.6%; it dominated or co-dominated the herbaceous flora at 11 sites. Areas and locations (UTM coordinates) for each patch may be found in Appendix A. Species lists are available for each fragment in the Appendix C.

#### *PCA on landscape and geologic variables*

Our study sites described a continuum from relatively rural landscapes with large areas of well connected forest to suburban landscapes dominated by housing development and including only small, isolated forest patches. Population density

ranged from 0.5 people/ha around Oxbow Park to 35.8 people/ha in Portland's western suburbs. Table 2-3 presents correlations between the individual environmental variables, as well as correlations between PCA axes.

We retained three PCA axes from the landscape analysis that accounted for 86.6% of the variation in landscape composition (Table 2-4). The first axis (*LAND1*) represented a gradient of increasing urbanization and decreasing forest cover. Sites with negative scores on this axis had larger proportions of forest in their buffers and more connectivity among forest patches across the landscape. In contrast, high scoring sites were located in dense suburban residential developments. This axis also correlated with the proximity values of individual study fragments (Table 2-3). Sites in more fragmented landscapes were themselves more isolated. Because these two measures of isolation were essentially redundant in our dataset, *PROX* was dropped from subsequent analyses, and *LAND1* was used as an indicator of patch isolation as well as urbanization. The second axis (*LAND2*) segregated landscapes containing large portions of developed canopy from those that contained higher amounts of treeless open space (*OPEN*; positive scores). *LAND3* separated relatively commercial or industrial landscapes from landscapes with primarily open habitat.

Along the first geologic axis (*GEO1*), fragments varied from low elevation, relatively flat sites with simple topography to higher elevation locations with greater relief, steep slopes, and high stream densities (Table 2-4). The second axis (*GEO2*) described a gradient of increasing wetland density, but was also moderately correlated with increasing stream density and lower elevations. We interpreted it as a gradient of

increasingly mesic soil conditions. The third geologic axis (*GEO3*) indicated the average slope within a site's sample plots, independent of its elevation, overall relief, or hydrology. Sites with high positive scores contained plots located on steeper slopes. In all, the PCA captured 83.4% of the geologic variation between study sites.

*Richness and diversity: multiple regression*

Spatial patterns explained from 12.4-43.4% of the variation in plant species richness and Shannon diversity (Table 2-5). Environmental variables explained from 0.0-41.1% of the remaining variation after removing the effects of spatial covariables. Woody species richness and diversity was principally influenced by patch area and shape. As patches became smaller and their shapes grew more convoluted, native trees and shrubs lost diversity while non-natives increased in both diversity and richness. In addition, both exotic species richness and overall diversity increased as site aspects became more southwesterly and exposed to sunlight (low *ASPECT*). Overall woody species richness declined marginally with increased distance from trails (i.e. increased with trail density). In general, non-native species richness and diversity varied more strongly with environmental variables than did native richness and diversity.

Herbs were primarily influenced by topography (*GEO1*) and surrounding land use (*LAND3*), although non-native richness and diversity correlated with patch area instead (Table 2-5). The species richness and diversity of native herbs and herbs overall increased as patches became more rugged (high *GEO1*). Overall richness and

native richness and diversity also declined with greater proportions of commercial-industrial land use in the matrix. Non-natives achieved higher richness and diversity in smaller patches.

### *Constrained ordinations*

Figures 2-2 to 2-4 illustrate the results of PCCAs on woody composition, herbaceous composition, and vegetation structure, respectively, in relation to patch, landscape, and geologic gradients. Because of the short gradients involved in our study, the biplots can be interpreted in linear, rather than unimodal terms (ter Braak and Smilauer 2002). This means that an arrow drawn from the origin to a species point would indicate the direction in which the species increased in abundance. It also means that species near the center of the graph are more evenly distributed among sites than those on the periphery. Only ordinations describing the effects of environmental variation after controlling for spatial covariables are presented.

The main gradients influencing floristic composition of trees and shrubs were combinations of land use around the sites, topographic complexity, and patch size (Fig. 2-2). Together, they explained 29.4% of the variation in species composition. Two distinct native communities were apparent in the larger fragments, clearly illustrating our study's location at the interface of the Western Hemlock and Willamette Valley vegetation zones (ellipses in Fig. 2-2). Species associated with the mesic forests of the Oregon Coast Range and the Western Cascades were clustered on the far right of the first axis. These included shade tolerant, climax tree species such

as Western hemlock (*TSHE*), Grand fir (*ABGR*), and Western red cedar (*THPL*), as well as shrubs such as salmonberry (*Rubus spectabilis*, *RUSP*) and red huckleberry (*Vaccinium parvifolium*, *VAPA*). Communities characterized by such species were often found in large, topographically complex fragments amidst heavily forested, well connected landscapes.

Species such as ponderosa pine (*Pinus ponderosa*, *PIPO*), Oregon oak (*Quercus garryana*, *QUGA*), and Oregon ash (*FRLA*), which were associated with the Willamette Valley vegetation zone, formed a cluster on the second axis toward the top of Fig. 2-2. These species were also more common in larger fragments, but tended to occur in smaller fragments than the late-seral Western hemlock associates. Willamette valley species were most common on flatter, lower elevation sites in more open, less heavily forested landscapes. They were relatively unaffected by urbanization (*LAND1*), but tended to occur in open, rather than commercial landscapes (high *LAND2*, low *LAND3*).

As patch size declined, the plant community was increasingly dominated by species that were common throughout most or all of the 48 sites. This is apparent in the skewed distribution of uncommon species (distant from the origin), which form tails coinciding with the arrow for patch area instead of spreading evenly across Fig. 2-2. The species in smaller sites included early- to mid-seral, disturbance-related trees, such as Douglas fir (*PSME*), big-leaf maple (*ACMA*), other hardwoods (e.g. *ALRU*, *ACCI*, *COCO*), and several common shrubs (e.g. *POMU*, *SARA*, *BENE*, *RUPA*) that can occur in both vegetation zones. Non-natives (circles in Fig. 2-2)

formed a distinct band perpendicular to the fragment area vector and located just below the mean patch size, which occurs at the origin. They were positively associated with smaller patches, increased urbanization, and decreased forest connectivity (*LANDI*). To a lesser extent, they were associated with commercial or industrial landscapes.

The PCCA for herbs explained a lower proportion of the variance (11.5%) than for woody species (Fig. 2-3). The main gradient influencing herbs was defined by patch area and water availability (*GEO2*). Most of the common species were more-or-less ubiquitous, as indicated by their locations near the center of the graph. However, one species (*TEGR*) was found primarily in somewhat smaller, drier sites, and three were found in larger, wetter sites (*VAHE*, *TROV*, and *DIHO*). The bulk of the less common species were also encountered more frequently in larger, wetter sites. Non-native species did not follow this pattern, with 6 of the 7 exotics in the ordination occurring in smaller, more xeric patches.

A second gradient, defined by *LAND2* and *ASPECT*, also influenced herbaceous community composition. Sites with high positive scores on this axis were more exposed to the drying effects of solar radiation, with southwestern aspects and little canopy cover in the matrix around the sites (Fig. 2-3, *LAND2*). Such sites contained relatively shade-intolerant plants, such as *Urtica dioica* (*URDI*) and *Vicia spp* (*VISP*). Low scoring sites had northeastern aspects and high proportions of developed canopy in their buffers. They tended to contain species more typical of interior forests, such as *Adiantum pedatum* (*ADPE*). As would be expected given the low variance

explained by the ordination, however, not all species followed these patterns. *Asarum caudatum* (ASCA), for example, is typically associated with shaded forests but occurred in relatively exposed (albeit large, wet) sites.

Three variables, *AREA*, *LAND2*, and *GEO2*, explained 16.7% of the variation in forest structure among our sites (Fig. 2-4). For clarity, Fig. 2-4 shows only those aspects of forest structure for which the ordination explained > 10% of their variation. Larger patches with more canopy cover in their buffers contained greater quantities of coarse woody debris, including both logs and snags. This was especially true for class 5 coarse woody debris. These sites contained more very large trees (*DBH5*) and deeper litter layers (*LDEEP*). On average, hardwoods in these sites had greater overall importance values than conifers. At the right side of the first axis, small sites with open buffers (high *LAND2*) contained more conifers, greater overall total basal areas, and more stems. Small and mid-sized trees (*DBH1*, *DBH3*) were associated with these sites, as were ground level shrubs (*SHRBI*) and sticks and twigs (*SWD*). The amount of bare rock at a site (*ROCK*), the amount of climbing English ivy (*IVY*), class 4 logs (*LOGV4*), and, to a lesser extent, class 3 logs (*LOGV3*) all increased with wetland density (*GEO2*). Low elevation, wetland sites contained few very large trees (*DBH5*).

## Discussion

Both patch size and landscape context were important determinants of forest structure, community composition, and richness in developed landscapes. As might be expected (Ohmann and Spies 1998), the landforms underlying Portland area forests

shaped their community composition to a large extent. Despite this influence, as patches became smaller and more urbanized, they lost their resemblance to mature Western Hemlock or Willamette Valley forests, and became homogenized. Non-native and disturbance-tolerant, early-seral species dominated these more developed sites. Despite this overall pattern of disturbance and simplification, changes in patch characteristics, landscape composition, and geology affected different segments of the community in distinct ways. This was evident in both the different responses of native and non-native species richness and diversity, and the ordinations. Although the patterns were not surprising, given the variable life histories of the plants that we studied, there are several possible mechanisms that may have contributed to their formation.

### *Woody Species*

After removing the effects of spatial covariables, mean native diversity increased with patch size and declined in sites with more convoluted shapes (Table 2-5). We did not find any significant relationship between patch area and native species richness. This contrasts with other studies in urban forests, which have found strong species-area relationships (e.g. Hoehne 1981, Hobbs 1988). The difference may have resulted from our decision to use mean species richness per plot, rather than total site richness (cf. Ross *et al.* 2002). Our measure minimized the influence of habitat heterogeneity within patches by focusing on richness at specific microsites. Alternatively, the failure of earlier authors to account for spatial patterns in their datasets might have

inflated area effects if both area and richness were spatially structured (Borcard *et al.* 1992, Fortin and Gurevitch 2001). While we do not know whether such patterns existed in previous studies, large urban forest fragments are often located on the periphery of cities.

The primary gradient influencing tree and shrub composition ran from large, well connected fragments in heavily forested, topographically complex landscapes to smaller, flatter, more isolated patches in urbanized, valley floor locations (Fig. 2-2). Upland mesic forest species such as western hemlock, grand fir, and western red cedar were more likely to be found in large, topographically complex fragments occupying heavily forested, well connected landscapes. Lowland Willamette Valley species such as Oregon white oak, Oregon ash, serviceberry (*Amelanchier alnifolia*), and black hawthorn (*Crataegus douglasii*) were found in flatter, lower elevation locations in more open landscapes. These sites presumably had warmer microclimates, more light, and greater groundwater access. They were also more heavily urbanized, probably due to the availability of level construction sites. The lowland species were less strongly associated with patch size than the Western Hemlock community, but this was probably an artifact of our sample, which included only one Willamette Valley site > 100 ha in area.

As patch size declined, specialized or late-successional species from both associations disappeared, leaving regionally common, disturbance-tolerant, photophyllic species, such as Douglas fir, big-leaf maple, and other hardwoods. These early- to mid-seral tree species dominate relatively young forests in western Oregon.

In Portland, they are also among the most frequent native tree species in the matrix. Douglas fir in particular is common to many parks and residential properties, and contributes to much of the canopy cover in developed areas (N.I.L. pers. observ.). Non-native trees and shrubs also occurred more frequently in small, urbanized patches (Fig. 2-2), and increased in richness and diversity as patches became smaller and more edge-heavy (Table 2-5). Similarly, invasion by *Prunus serotina*, a North American cherry, increased in small forest patches in Brussels (Honnay *et al.* 1999a). These results strongly imply that non-natives originated in the matrix and invaded patches as a function of their relative edge length.

Concurrent with the loss of late-seral trees and shrubs, smaller patches became structurally simplified. They contained less coarse woody debris, fewer very large trees (*DBH5*), and shallower litter layers. Paradoxically, these sites were also dominated by conifers, while hardwoods, usually considered pioneers in this region, were more prevalent in larger sites. However, this was largely due to the absence of hardwoods from small sites, which contained mainly Douglas fir. Large sites, while containing more mixed communities, also included a greater diversity of coniferous trees, including shade-tolerant species. These changes in forest structure have the potential to affect a wide variety of wildlife, including small mammals (Hallett *et al.* 2003, Smith *et al.* 2003).

In addition to topography, water availability, and fragmentation by urban development, canopy cover around patches correlated with community composition and forest structure (Fig. 2-2, see also *Non-native Invasions*, below). *A posteriori*

analysis of adjacency tables created by FRAGSTATS showed that both treeless open spaces and developed canopy shared edges with forest more frequently than other land uses (1-way ANOVA, Tukey HSD: all  $P < 0.001$  for *DCAN*,  $P < 0.004$  for *OPEN*; *OPEN* vs. *RES*,  $P = 0.169$ ;  $n = 48$ ). In combination with the species found at these sites, the adjacency tables suggest that land use around urban forest patches, and canopy tree retention in particular, may influence forest composition by moderating microclimatic edge effects. However, these correlations could also be coincidental, since more canopy cover has been retained in the West Hills than in the lowlands, where open-canopy associates were presumably historically more common.

### *Herb Species*

Overall, the measured environmental variables explained a low proportion of the variability in herb species richness and composition after controlling for spatial effects. These results contrast with findings from other cities, where native herbs showed strong species-area effects (Hobbs 1988, Godefroid and Koedam 2003). As with the woody species, this could be a consequence of our use of mean species richness (cf. Ross *et al.* 2002), or of our removal of spatial effects. In addition, our surveys were conducted in mid- to late summer and probably missed ephemeral spring herbs. Local conditions at sample plots may have also had a larger influence on the herbs than on woody species. Although we detected differences in the tree communities among sites, the overall dominance of Douglas fir and big-leaf maple in most locations may help explain the lack of strong patterns in the herb community.

However, native richness and diversity increased with greater topographic complexity. This may have resulted from the correlation between *GEO1* and *AREA* (Table 2-3; although below our cutoff of 0.7, collinearity between these variables may have also contributed to the lack of a significant area effect), but the most likely possibility is that topographically complex patches would contain a greater variety of microsites.

Non-native species richness and diversity increased in small patches, and common non-natives (i.e. those that were included in ordinations) occurred more frequently in smaller, drier, higher elevation sites (low *GEO2*). Several common weeds were also associated with less developed canopy (Fig. 2-3, *LAND2*). In contrast, most common natives occurred in larger, wetter locations, although *LAND2* and *ASPECT* also affected their distribution in the ordination (Fig. 2-3). This reinforces the interpretation that tree retention in the matrix affects forest microclimate. Species associated with lighter conditions and forest gaps (e.g. *URDI*, *VISP*) occurred in sites with southwestern exposure and little surrounding canopy, and typical forest interior species (e.g. *TROV*, *ADPE*) tended more toward locations shaded by both aspect and landscape-level tree cover. Not all species conformed to these trends (e.g. *ASCA*), but this may have been due to an attenuation of edge effects in larger fragments. Interestingly, native richness and diversity also declined in more commercial landscapes. The reason for this is unclear, although the positive association between *GEO3* and English ivy (Fig. 2-2, *HEHE*) suggests that competition may be partly responsible (see *Non-native invasions*, below).

*Mechanisms influencing urban forests*

The patterns we detected are consistent with several other studies on fragmented plant communities in urban settings (e.g. Hobbs 1988, Honnay *et al.* 1999b, Duncan and Young 2000, Malmivaara *et al.* 2002, Godefroid and Koedam 2003), and point to several mechanisms that might drive forest community structure in urban environments. All are competition-based, and while the dominance of some of our plots by English ivy and Himalayan blackberry indicates that competition is important in Portland forests, it does not allow us to distinguish between these mechanisms. They are also not exclusive and probably reinforce one another.

Studies of species richness have indicated that patch area may affect forest plant communities in urbanized landscapes through an increased influence of the matrix on small fragments (Hobbs 1988, Honnay *et al.* 1999b, Godefroid and Koedam 2003). Strong matrix effects on small fragments have also been noted in rural studies (Esseen 1994), and smaller habitat islands are generally assumed to be more vulnerable to extrinsic disturbances (McArthur and Wilson 1967). However, disturbances such as trampling may be more intense in urban matrices, especially at edges (Matlack 1993). Moderate trampling can favor quickly growing, clonal, or pioneer species (Littlemore and Barker 2001, Malmivaara *et al.* 2002). Trampling and soil disturbance altered species frequencies even at relatively low intensities in suburban Finnish forests, particularly in small sites (Malmivaara *et al.* 2002). Anthropogenic disturbance was also found to accelerate invasion and native species loss in fragmented eucalypt forests in Australia (Ross *et al.* 2002).

We did not find any direct evidence of negative disturbance effects after correcting for broad scale spatial patterns. In fact, trail density had a very slight, but significant positive influence on overall woody species richness. Our method of measuring disturbance (average distance to nearest trail) was fairly crude, and techniques that account for the frequency of visitation might produce different results. In addition, the most intense effects of human disturbance are usually localized to trail edges (Bhujra and Ohsawa 1998, Malmivaara *et al.* 2002). They may not have been apparent at the patch scale. In regressions conducted without correcting for spatial effects, non-native herbs increased in both richness and diversity as the distance to the nearest trail declined (richness: partial  $R^2 = -0.383$ ,  $P = 0.008$ ; diversity: partial  $R^2 = -0.265$ ,  $P = 0.071$ ). These results are consistent with the idea that anthropogenic disturbance drives compositional changes. This effect may have been masked by the removal of spatial effects if trail density varies strongly with space.

A second potential mechanism relates to species' abilities to live in the matrix. A low tolerance for matrix habitats can predict vulnerability to fragmentation (Gascon *et al.* 1999a), in part because colonization from the matrix may drive species composition in small or edge-heavy patches. Because early-seral and non-native species are more common in the matrix, they could have an advantage over less disturbance-tolerant species in colonizing fragments. Once nearby pioneers or non-natives invade a site, they may stall succession by spreading quickly *in situ* and monopolizing the available resources (see Non-native Invasion, below, Yao *et al.* 1999).

Our results suggest that something similar to this may have occurred in Portland forest fragments. As would be expected under this mechanism, non-native trees, shrubs, and herbs increased in diversity as patches became smaller and as their shapes became more convoluted (i.e. patches became more vulnerable to edge-influenced colonization, Table 2-5). Native trees lost diversity under similar conditions. In addition, late-seral species were lost and non-natives gained as landscapes became more fragmented by urbanization and patches became more isolated (Fig. 2-2). These patterns suggest that seed dispersal in this landscape may occur over relatively short distances, so that species in the matrix are more likely to reach isolated patches. However, specific information on recruitment and seed dispersal patterns would be needed to conclusively test this hypothesis.

A plant's mode of dispersal might also be expected to influence its success under this mechanism. However, while zoochorous species travel further and colonize patches more rapidly than wind-dispersed species (Yao *et al.* 1999), zoochorous forest interior species are also more likely to use agents whose movements are restricted by fragmentation. This can negatively affect their prevalence in fragmented landscapes (Metzger 2000). Generalist birds disperse many of the fruit-bearing species in our study, but these birds are presumably at least as likely to disperse matrix based species as forest interior species, especially in highly developed landscapes. The conifers are primarily dispersed by wind or by squirrels, and the latter may well be affected by fragmentation (Chapter 2, Lomolino and Perault 2000, Goheen *et al.* 2003). Dispersal

mode had no effect on plant extinction probability in urban habitat fragments in New Zealand (Duncan and Young 2000).

Finally, changes in the abiotic environment, such as edge related nutrient fluxes and microclimatic changes, might have favored early-seral species over forest interior specialists. Urban forest edges concentrate and accumulate airborne nutrients such as inorganic nitrogen (Weathers *et al.* 2001), and small or edge-heavy fragments receive more solar radiation (Collinge 1996). Although the relationship between productivity and diversity is complex, resource supplementation should confer an advantage on species that respond quickly to surpluses, allowing them to overgrow and out-compete competitors (Tilman 1994, Rajaniemi 2003). Competitive interactions have been implicated in the loss of shade tolerant species in Amazonian forest fragments and the absence of ancient woodland herbs from small, urban forest patches in Belgium (Honnay *et al.* 1999b, Metzger 2000, Godefroid and Koedam 2003). Because we did not measure resource levels directly, we can only speculate as to their importance in Portland. However, the high stem densities and dense ground-level (< 0.5 m) shrub growth in small patches with more open matrices suggests that more light was penetrating into these sites (Fig. 2-4). In addition, the association between non-native richness and southern exposure, in combination with smaller, more edge-heavy sites, implies that many non-native weeds in our study responded well to high light conditions (Table 2-5).

Our analysis did not account for site histories. However, community composition and physical forest structure indicated that larger fragments occupied later

successional stages than smaller sites (Fig. 2-4). Large patches contained deeper litter layers and more coarse woody debris, especially in higher decay classes. They also contained more old trees (*DBH5*) and shade-tolerant conifers (e.g. western red cedar, grand fir), indicating a less intense disturbance history or greater recovery time.

Previous land use at a site can significantly affect forest composition, as can stand age (e.g. Honnay *et al.* 1999a, Ross *et al.* 2002, Aragon and Morales 2003). Moreover, long-lived trees introduce substantial time lags into analyses, since they may have become established under much different conditions than currently exist (Duncan and Young 2000, Metzger 2000). Because some sites have been isolated longer than others and have histories of active management, including deliberate tree planting, grazing, and fire management (Broshot 1999), our results may say more about the effects of patch history than they do about current environmental conditions.

Surveying specifically for new recruitment might help to unravel this issue (Duncan and Young 2000, Metzger 2000), although a detailed historical analysis would probably be needed to develop a complete picture.

#### *Non-native invasion of urban forests*

Exotic species formed a relatively small, but significant portion of the overall plant community in Portland forests. Many of the same factors that led to early-seral dominance in small fragments probably also facilitated invasion by matrix-based non-natives. As groups, exotic and native species showed opposite responses to fragmentation, with non-natives increasing in small, isolated, more edge-heavy, urban

sites (Table 2-5, Fig. 2-2, 2-3). These associations imply that invasions in these patches have occurred mainly as edge effects. Among woody species, exotic richness and diversity were also better predicted by current environmental conditions than by spatial patterns (see  $R^2$ -values in Table 2-5). If the native tree community reflects residual historical trends, the stronger response to current conditions among exotics surely indicates that invasion has been a fairly recent phenomenon.

The three most common exotic shrubs in our study, English ivy, Himalayan blackberry, and holly, appear well suited to life in small urban forests characterized by frequent disturbance and patch isolation. All three species are relatively resistant to mechanical damage, regrow following disturbance, and bear fruits whose seeds are transported by ubiquitous, generalist birds such as the American robin (*Turdus migratorius*). All three species were common in the matrix (pers. observ.). The first two spread clonally, and the latter pair actively resist casual human disturbance with thorns or sharp edged leaves. If anthropogenic disturbance is truly a driving factor in urban systems, then we would expect urban invasives in other parts of the world to possess similar characteristics.

Many non-native plants have been used for landscaping in Portland, especially in commercial areas, and this is consistent with the increased richness and diversity as patches became smaller, more convoluted, and more isolated (see also Collinge 1996, Ross *et al.* 2002, Aragon and Morales 2003). Invasion by these species may help explain the negative associations between overall herb richness and native richness and diversity, and commercial land use (Table 2-5). English ivy was also associated

with commercial development (Fig. 2-2; *HEHE*) and completely blanketed the forest floor in some cases, excluding almost all new growth.

Ivy also increased with canopy cover in the matrix. This suggests that developed forest may provide an intermediate step between the matrix proper and the more sheltered, shaded environment of the forest. Ground level disturbance in these areas may provide shade tolerant invaders with an opening that they would not otherwise receive in diverse forest interior communities (Brothers and Spingarn 1992). Once established, such a nucleus could serve as a beachhead for invasion of the forest (With 2002), especially if bird dispersers are more common in locations with more canopy cover (Hennings and Edge 2003).

### **Conclusions and Management Implications**

Fragmentation and edge effects appear to play important roles in Portland area forests. Smaller or more convoluted sites contained more exotic plant species and less diverse native tree communities. Although our observational approach precludes firm conclusions about causal relationships, the patterns described above suggest several possible mechanisms that may influence the ecology of forests in urbanized areas. As forested landscapes become fragmented, the smaller, more isolated patches may become increasingly subject to matrix-based influences, including anthropogenic disturbance, resource supplementation, and invasion by matrix-friendly species (see reviews by Murcia 1995, Collinge 1996, Jules and Shahani 2003). In Portland, late-seral or shade-tolerant species found in unfragmented landscapes and larger patches

were replaced by fast-growing, disturbance-associated generalists and non-natives in small, isolated fragments. These forest patches were also structurally simplified, with less coarse woody debris, more young trees, and heavier ground level shrub growth, indicating greater light penetration.

Our results also suggest that land uses adjacent to forests may influence species composition by modifying microclimatic conditions within patches. Retaining substantial tree cover around forest patches could buffer the fragment against increased wind and solar radiation. This may help to maintain some native communities. However, areas of canopy with disturbed understories may also serve as dispersal nuclei, facilitating the entry of non-native species into forests.

All of these hypotheses require additional attention. In particular, controlled experiments are needed to determine how anthropogenic disturbance, resource subsidies, and seed dispersal vary with fragmentation and landscape composition, and to relate these factors directly to long term successional patterns in urban forests. Even in the absence of further research, however, our results provide several suggestions for the management and conservation of forest communities in urbanizing landscapes. Wherever possible, large areas of forest should be retained to provide refuges for specialist species. However, maintaining these species in smaller patches may be possible, provided that landscaping decisions adjacent to forest preserves complement management goals. Managers should therefore consider implementing programs to encourage land uses that will help maintain microclimates favorable to the target community. At the same time, nearby land owners should be educated

concerning invasive plants (especially English ivy, Himalayan blackberry, and English holly), and encouraged to remove them wherever possible. Finally, active creation of structural features typical of older, more mature forests (e.g. logs) may create microenvironments favorable to some species.

TABLE 2-1: Forest structural variables measured in 48 forest fragments in Portland, Oregon.

Code	Definition	Mean	SE	CV
<b>Ground Cover</b>				
<i>HERB</i>	Herb cover (%)	25.46	15.35	60
<i>MOSS</i>	Moss cover (%)	21.61	12.81	59
<i>SOIL</i>	Bare soil (%)	13.35	8.61	65
<i>ROCK</i>	Exposed rock (%)	0.88	1.83	208
<i>SWD</i>	Sticks and twigs, <2.5 cm diameter (%)	68.89	17.67	26
<i>LWD</i>	Woody debris, 2.5 - 10 cm diameter (%)	10.00	3.13	31
<i>LEAF</i>	Leaf Litter Cover (%)	92.87	5.96	6
<i>LDEEP</i>	Leaf Litter Depth (cm)	2.24	1.55	69
<b>Shrubs</b>				
<i>SHRB1</i>	Shrub density, 0.0 - 0.5 m (average number of hits)	2.52	0.91	36
<i>SHRB2</i>	Shrub density, 0.5 - 1.0 m (average number of hits)	1.12	0.34	30
<i>SHRB3</i>	Shrub density, 1.0 - 1.5 m (average number of hits)	0.58	0.25	42
<i>SHRB4</i>	Shrub density, 1.5 - 2.0 m (average number of hits)	0.46	0.22	48
<i>SHRB5</i>	Shrub density, 2.0 - 2.5 m (average number of hits)	0.44	0.18	41
<i>SHRB6</i>	Shrub density, 2.5 - 3.0 m (average number of hits)	0.44	0.20	46
<b>Trees</b>				
<i>CANPY</i>	Canopy Closure (%)	67.81	6.95	10
<i>BASAL</i>	Total basal area of trees with DBH > 2.5 cm (m <sup>2</sup> /ha)	57.99	16.55	29
<i>STEMS</i>	Total stem count	29.26	14.38	49
<i>DBH1</i>	Stem count, DBH 2.5 - 10.0 cm	18.85	13.69	73
<i>DBH2</i>	Stem count, DBH 10.1 - 30.0 cm	5.24	3.16	60
<i>DBH3</i>	Stem count, DBH 30.1 - 60.0 cm	4.03	1.48	37
<i>DBH4</i>	Stem count, DBH 60.1 - 100 cm	1.42	0.81	57
<i>DBH5</i>	Stem count, DBH > 100 cm	0.08	0.13	171
<i>IVY</i>	Stem count with English ivy over 3 m	2.16	2.77	128
<i>CONES</i>	Total importance value of conifers (0 - 100)	17.73	11.70	66

Table 2-1 (cont.):

<i>HARDW</i>	Total importance value of angiosperms (0 - 100)	10.55	6.70	64
Coarse Woody Debris				
<i>CWD</i>	Total volume of coarse woody debris (m <sup>3</sup> /ha)	214.8	166.7	78
<i>LOGT</i>	Total volume of logs (m <sup>3</sup> /ha)	43.5	42.6	98
<i>SNAGT</i>	Total volume of snags (m <sup>3</sup> /ha)	31.4	24.1	77
<i>LOGV1</i>	Logs with intact bark and branches (m <sup>3</sup> /ha)	8.6	11.7	137
<i>LOGV2</i>	Logs with loose bark, outer wood solid (m <sup>3</sup> /ha)	25.5	69.0	270
<i>LOGV3</i>	Logs, bark entirely missing, inner wood solid (m <sup>3</sup> /ha)	14.7	36.6	250
<i>LOGV4</i>	Logs, outer wood soft, inner wood solid (m <sup>3</sup> /ha)	11.9	18.2	153
<i>LOGV5</i>	Logs, soft throughout (m <sup>3</sup> /ha)	21.1	26.7	126
<i>SNAGV1</i>	Snags with intact bark and branches (m <sup>3</sup> /ha)	21.1	37.2	176
<i>SNAGV2</i>	Snags with loose bark, outer wood solid (m <sup>3</sup> /ha)	12.2	14.4	118
<i>SNAGV3</i>	Snags, bark entirely missing, inner wood solid (m <sup>3</sup> /ha)	6.3	9.6	151
<i>SNAGV4</i>	Snags, outer wood soft, inner wood solid (m <sup>3</sup> /ha)	7.5	14.5	194
<i>SNAGV5</i>	Snags, soft throughout (m <sup>3</sup> /ha)	11.1	14.3	129

TABLE 2-2: Codes, definitions, and descriptive statistics for environmental variables used in regressions and constrained ordinations ( $n = 48$ ).

Code	Definition	Mean	S.D.	CV
<b>Patch</b>				
<i>AREA*</i>	Patch area (ha)	88	249.9	284
<i>SHAPE</i>	Shape index (see text)	2.5	1.2	47
<i>PROX*</i>	Proximity index (see text)	1490	3933.6	264
<b>Landscape</b>				
<i>FOR</i>	Cover of forest in 1 km buffer (%)	15.2	7.8	51
<i>MNPROX*</i>	Mean proximity of all forest patches in 1 km buffer (see text)	694	2158.3	311
<i>DCAN</i>	Cover of developed canopy in 1 km buffer (%)	10.6	7.6	72
<i>AG<sup>†</sup></i>	Cover of agricultural fields in 1 km buffer (%)	1.8	3.9	216
<i>OPEN</i>	Cover of treeless open space in 1 km buffer (%)	7.5	7.8	104
<i>COM</i>	Cover of commercial/industrial land use in 1 km buffer (%)	14.5	6.1	42
<i>RES</i>	Cover of residential land use in 1 km buffer (%)	42.3	16.5	39
<i>WATER<sup>†</sup></i>	Cover of open water in 1 km buffer (%)	1.9	4.0	208
<i>UNDEF<sup>†</sup></i>	Cover of undefined land use in 1 km buffer (%)	0.5	0.5	103
<i>BUILD</i>	Building density in 1 km buffer (parcels/ha)	5.4	2.3	43
<i>POP</i>	Population density in 1 km buffer (people/ha)	15.2	7.3	48
<i>STRT</i>	Linear street density in 1 km buffer (m/ha)	113.0	39.6	35
<b>Geomorphic</b>				
<i>ELV</i>	Mean elevation (m)	122.5	55.1	45
<i>SLP</i>	Mean slope (degrees)	10.1	6.8	67
<i>RGELV</i>	Range of elevations sampled within a patch (m)	36.3	45.7	126
<i>ASPECT</i>	Cosine transformation of aspect (degrees, see text)	1.0	0.4	37
<i>WET*</i>	Wetland density (m <sup>2</sup> /ha)	310.7	988.0	318
<i>STRM*</i>	Linear stream density (m/ha)	175.2	381.9	218
<b>Anthropogenic Disturbance</b>				
<i>DTRAIL</i>	Average distance to the nearest trail from plot center (m)	27.0	23.8	88

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

<sup>†</sup> Excluded from analyses because of highly skewed distribution

TABLE 2-3: Pearson correlations between environmental variables for forest fragments in Portland, Oregon. See Table 2-2 and text for definitions and descriptions of data collection, and Table 2-4 for PCA axis loadings (*GEO1-3* and *LAND1-3*) ( $n = 48$ ).

	ELV	RGELV	SLP	ASPECT	WET	STRM	FOR	MNPROX	DCAN	COM	OPEN	RES
ELV	1.000											
RGELV	0.493*	1.000										
SLP	0.255	0.433*	1.000									
ASPECT	-0.029	0.079	0.208	1.000								
WET	-0.360*	-0.104	-0.130	-0.060	1.000							
STRM	0.265	0.632*	0.363*	0.018	0.029	1.000						
FOR	0.242	0.289	0.177	-0.070	-0.050	0.466*	1.000					
MNPROX	0.391*	0.606*	0.303*	-0.033	0.080	0.689*	0.757*	1.000				
DCAN	0.049	0.054	0.220	0.006	-0.222	0.203	0.373*	-0.001	1.000			
COM	-0.149	-0.013	-0.207	-0.138	-0.020	-0.090	-0.296	-0.151	-0.224	1.000		
OPEN	-0.123	-0.136	-0.118	-0.125	0.267	-0.169	-0.076	0.104	-0.601*	0.037	1.000	
RES	-0.198	-0.503*	-0.254	0.045	0.070	-0.575*	-0.721*	-0.811*	-0.149	-0.196	-0.097	1.000
BUILD	-0.014	-0.288*	-0.103	0.195	-0.015	-0.381*	-0.548*	-0.685*	0.131	-0.275	-0.176	0.825*
POP	-0.145	-0.348*	-0.208	0.127	0.000	-0.455*	-0.726*	-0.775*	-0.167	0.008	-0.056	0.841*
STRT	0.025	-0.226	0.047	0.132	-0.086	-0.359*	-0.419*	-0.627*	0.328*	-0.197	-0.262	0.683*
DTRAIL	0.306*	0.303*	0.261	-0.109	0.073	0.369*	0.168	0.309*	0.178	-0.131	-0.034	-0.213
AREA	0.295*	0.704*	0.417*	0.049	0.137	0.713*	0.418*	0.795*	-0.084	-0.138	-0.019	-0.626*
PROX	0.287*	0.555*	0.370*	-0.071	0.091	0.695*	0.760*	0.841*	0.303*	-0.219	-0.200	-0.677*
SHAPE	0.037	0.390*	0.395*	-0.056	0.101	0.532*	0.417*	0.615*	-0.078	-0.169	0.041	-0.458*
GEO1	0.693*	0.864*	0.659*	0.093	-0.308*	0.738*	0.389*	0.643*	0.192	-0.135	-0.211	-0.515*
GEO2	-0.434*	0.182	0.122	0.007	0.853*	0.440*	0.116	0.305*	-0.077	-0.015	0.148	-0.202
GEO3	-0.330*	-0.187	0.718*	0.211	-0.144	-0.170	-0.113	-0.219	0.183	-0.112	-0.040	0.094
LAND1	-0.175	-0.425*	-0.186	0.120	-0.018	-0.546*	-0.776*	-0.879*	-0.024	-0.062	-0.147	0.931*
LAND2	-0.199	-0.138	-0.269	-0.101	0.216	-0.254	-0.470*	-0.110	-0.894*	0.507*	0.705*	0.056
LAND3	-0.131	0.023	-0.085	-0.069	-0.193	-0.001	-0.206	-0.226	0.251	0.814*	-0.506*	-0.155

TABLE 2-3 (cont.):

	BUILD	POP	STRT	DTRAIL	AREA	PROX	SHAPE	GEO1	GEO2	GEO3	LAND1	LAND2	LAND3
BUILD	1.000												
POP	0.865*	1.000											
STRT	0.884*	0.691*	1.000										
DTRAIL	-0.042	-0.194	-0.022	1.000									
AREA	-0.486*	-0.481*	-0.518*	0.360*	1.000								
PROX	-0.512*	-0.686*	-0.380*	0.238	0.666*	1.000							
SHAPE	-0.403*	-0.406*	-0.444*	0.114	0.673*	0.614*	1.000						
GEO1	-0.262	-0.379*	-0.168	0.390*	0.684*	0.612*	0.429*	1.000					
GEO2	-0.210	-0.196	-0.243	0.155	0.419*	0.352*	0.371*	0.000	1.000				
GEO3	0.074	0.059	0.201	-0.062	-0.102	-0.092	0.129	0.000	0.000	1.000			
LAND1	0.920*	0.931*	0.823*	-0.178	-0.625*	-0.718*	-0.515*	-0.439*	-0.245	0.142	1.000		
LAND2	-0.225	0.129	-0.382*	-0.191	-0.041	-0.420*	-0.035	-0.298*	0.090	-0.126	0.000	1.000	
LAND3	-0.185	-0.027	-0.044	-0.090	-0.147	-0.100	-0.200	-0.030	-0.099	0.008	0.000	0.000	1.000

\* Significant at  $\alpha = 0.05$

TABLE 2-4: Variable loadings for landscape and geologic PCA analyses ( $n = 48$ ).

PCA Axis	% Var.	Variable													
		FOR	PROX	DCAN	COM	OPEN	RES	POP	BUILD	STRT	ELV	SLP	RGELV	WET	STRM
LAND1	51.7	-0.776	-0.879	0.024	0.062	0.148	0.931	0.931	0.920	0.823					
LAND2	22.3	-0.470	-0.110	-0.895	0.507	0.705	0.056	0.130	-0.225	-0.382					
LAND3	12.6	-0.207	-0.226	0.251	0.814	-0.506	-0.155	-0.028	-0.185	-0.044					
GEO1	46.0	0.693	0.659	0.864	-0.305									0.739	
GEO2	23.2	-0.434	0.122	0.182	0.855									0.439	
GEO3	14.2	-0.330	0.718	-0.187	-0.143									-0.171	

TABLE 2-5: Stepwise multiple regression of environmental factors associated with forest plant richness and diversity in Portland, Oregon forest fragments ( $n = 48$ ). Reported values represent adjusted  $R^2$  for spatial patterns and standardized regression coefficients and adjusted partial  $R^2$  after removing spatial effects for environmental variables.

	Mean	SE	Spatial		Environmental model with spatial covariables removed													
			$R^2$	$R^2$	AREA	SHAPE	ASPECT	GEOI	LAND3	DTRAIL								
<i>Woody Species</i>																		
Richness																		
Overall	10.23	1.64	0.434 <sup>†</sup>	0.069*														-0.262
Native	8.38	1.41	0.206 <sup>†</sup>															
Exotic	1.85	1.10	0.183 <sup>†</sup>	0.411 <sup>†</sup>	-0.779	0.301	-0.229											
Shannon Diversity																		
Overall	0.82	0.06	0.357 <sup>†</sup>	0.091 <sup>†</sup>														-0.301
Native	0.74	0.08	0.148 <sup>†</sup>	0.121*	0.470	-0.341												
Exotic	0.16	0.12	0.124 <sup>†</sup>	0.344 <sup>†</sup>	-0.794	0.375												
<i>Herb Species</i>																		
Richness																		
Overall	4.90	2.47	0.362 <sup>†</sup>	0.178 <sup>†</sup>					0.372	-0.325								
Native	3.81	2.19	0.345 <sup>†</sup>	0.267 <sup>†</sup>					0.367	-0.449								
Exotic	1.09	1.12	0.183 <sup>†</sup>	0.161 <sup>†</sup>	-0.401													
Shannon Diversity																		
Overall	0.48	0.22	0.276 <sup>†</sup>	0.130 <sup>†</sup>					0.361									
Native	0.40	0.21	0.267 <sup>†</sup>	0.186 <sup>†</sup>					0.363	-0.343								
Exotic	0.10	0.14	0.127 <sup>†</sup>	0.147 <sup>†</sup>	-0.383													

\* Significant at  $\alpha = 0.10$  † Significant at  $\alpha = 0.05$  ‡ Significant at  $\alpha = 0.001$

### Figure Legends

FIG. 2-1: Study area and location of 48 sites in Portland, Oregon at the confluence of the Columbia and Willamette Rivers. Numbers refer to site names in Appendix A.

FIG. 2-2: PCCA biplot of environmental effects on woody species composition in 48 urban forest fragments in Portland, Oregon, after controlling for spatial autocorrelation. The axes shown explain 24.9% of species variation. Triangles represent native species, circles represent non-natives. Dashed and solid ellipses designate Willamette Valley and Western Hemlock plant associations, respectively. Due to its scarcity, *Pinus ponderosa* (*PIPO*) was projected onto the axes *post-hoc*, and did not influence the ordination. See Appendix B and text for species codes.

FIG. 2-3: PCCA biplot of environmental effects on herb composition in 48 urban forest fragments in Portland, Oregon, after controlling for spatial autocorrelation. The axes shown explain 11.5% of species variation. Triangles represent native species, circles represent non-natives. See Appendix B and text for species codes.

FIG. 2-4: PCCA biplot of environmental effects on forest structure variables after controlling for spatial autocorrelation. The axes shown explain 15.5% of the variation. Only structural variables whose variance is explained to > 10% by environmental variation are shown. See codes in Table 2-1.

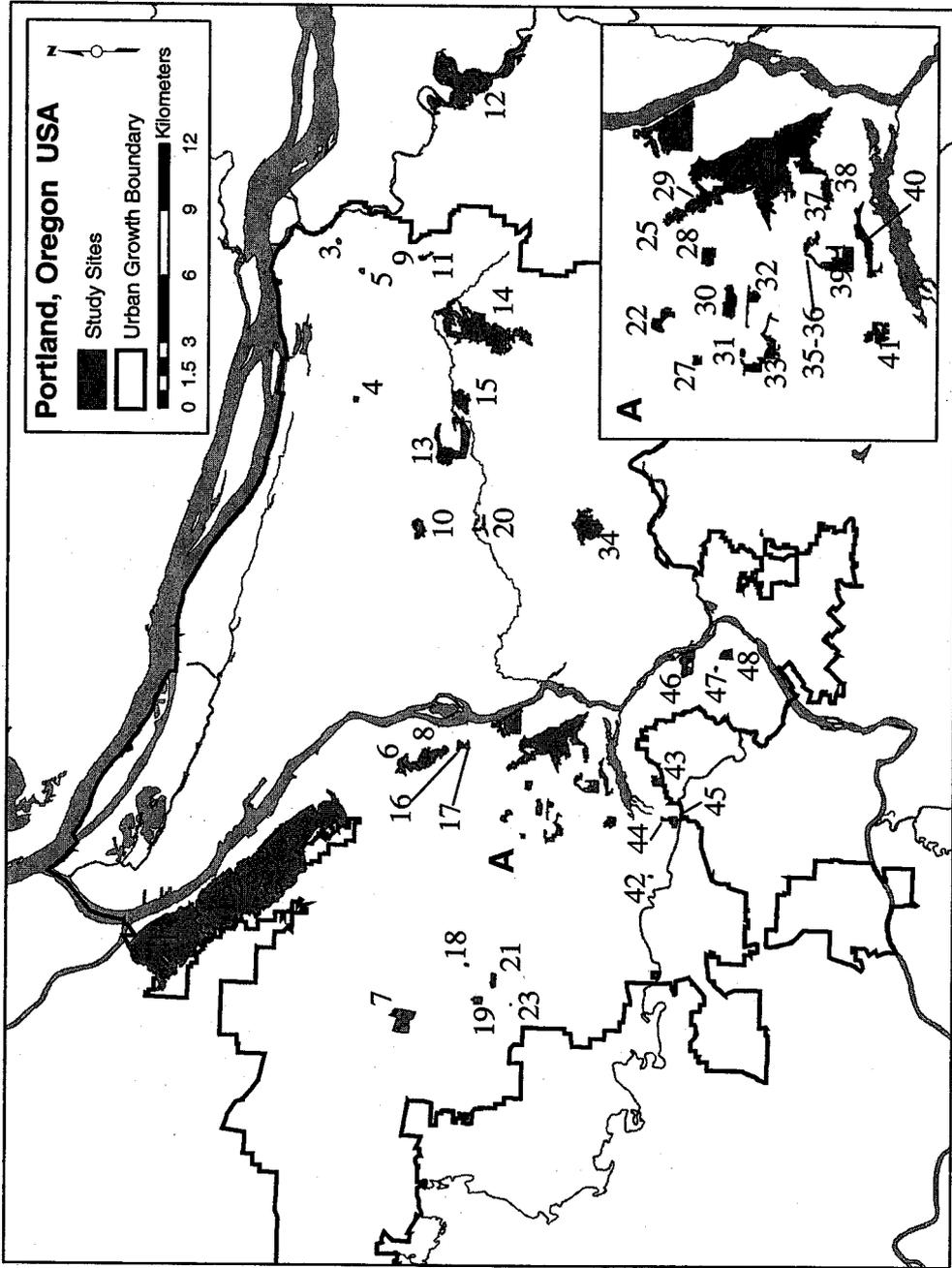


Fig. 2-1

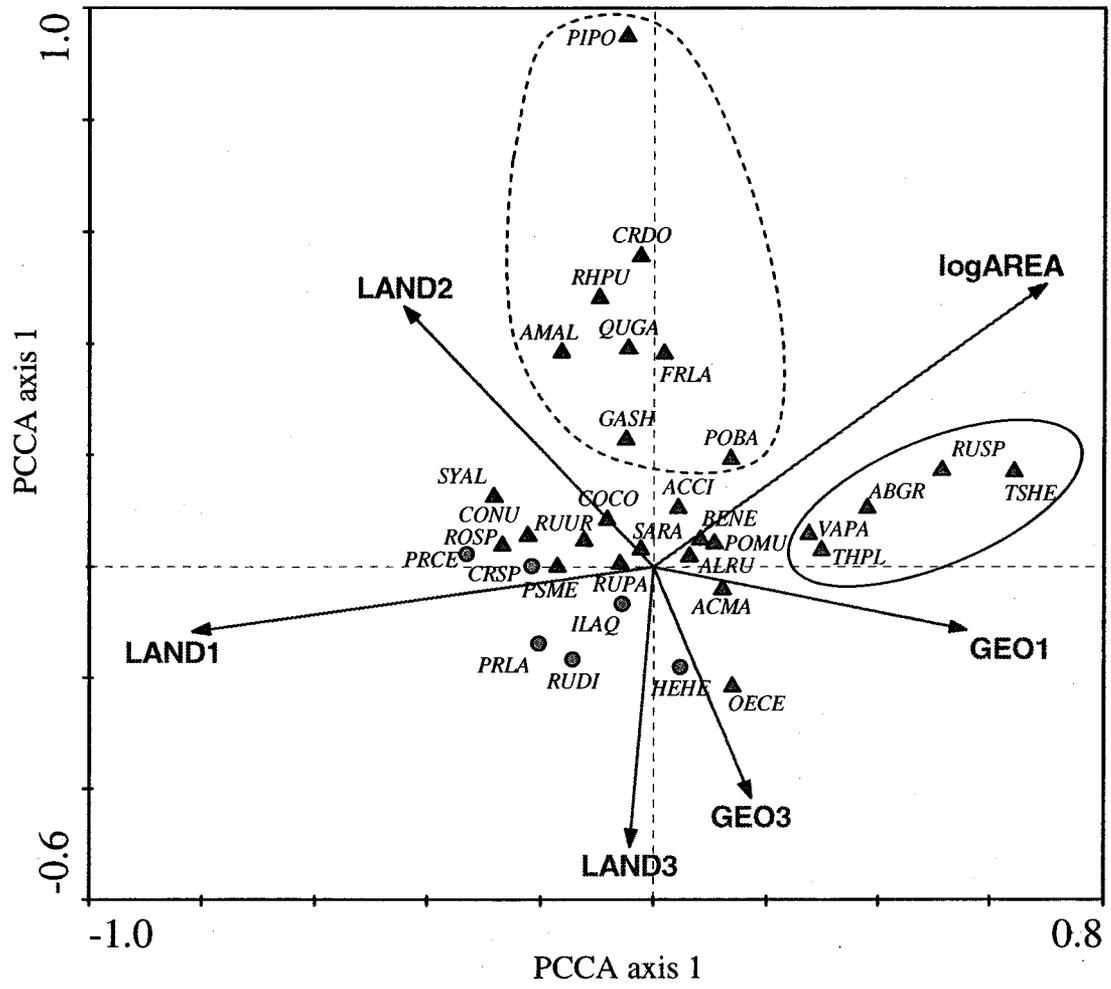


Fig. 2-2

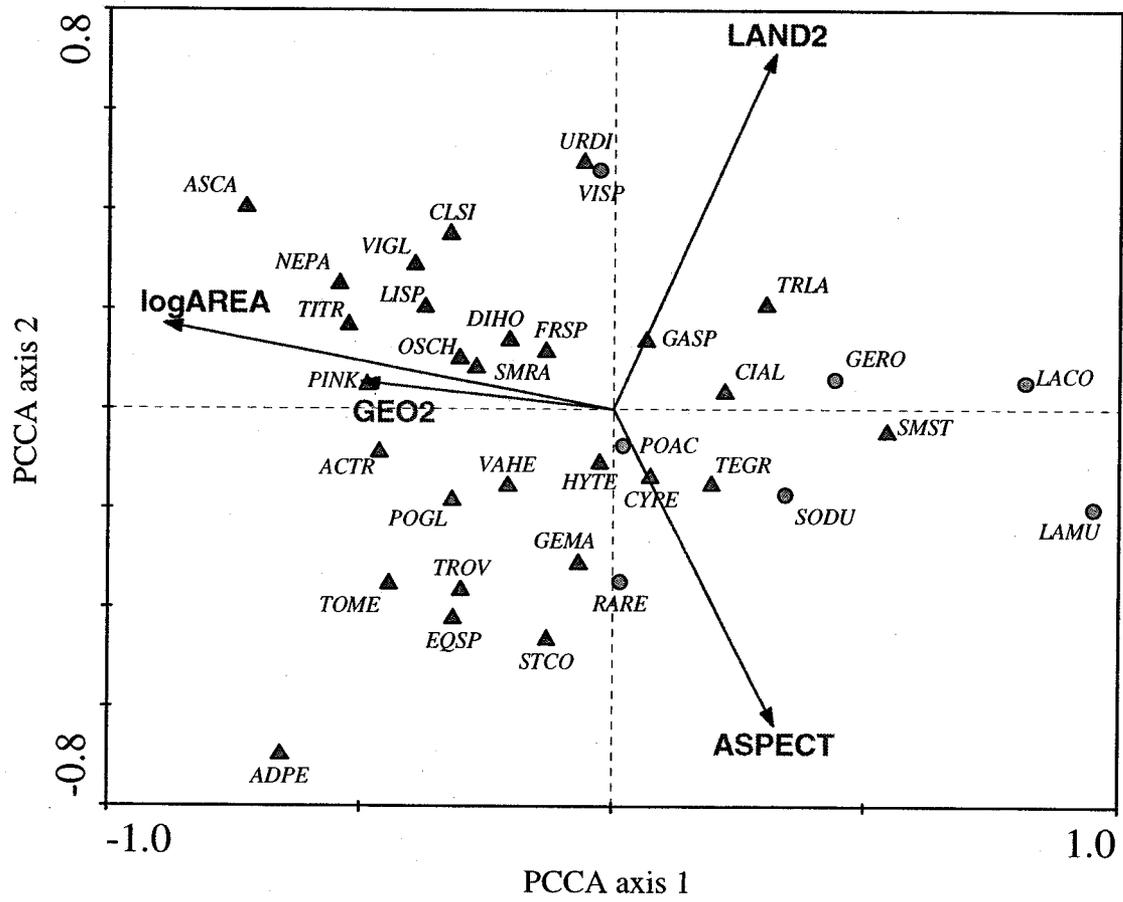


Fig. 2-3

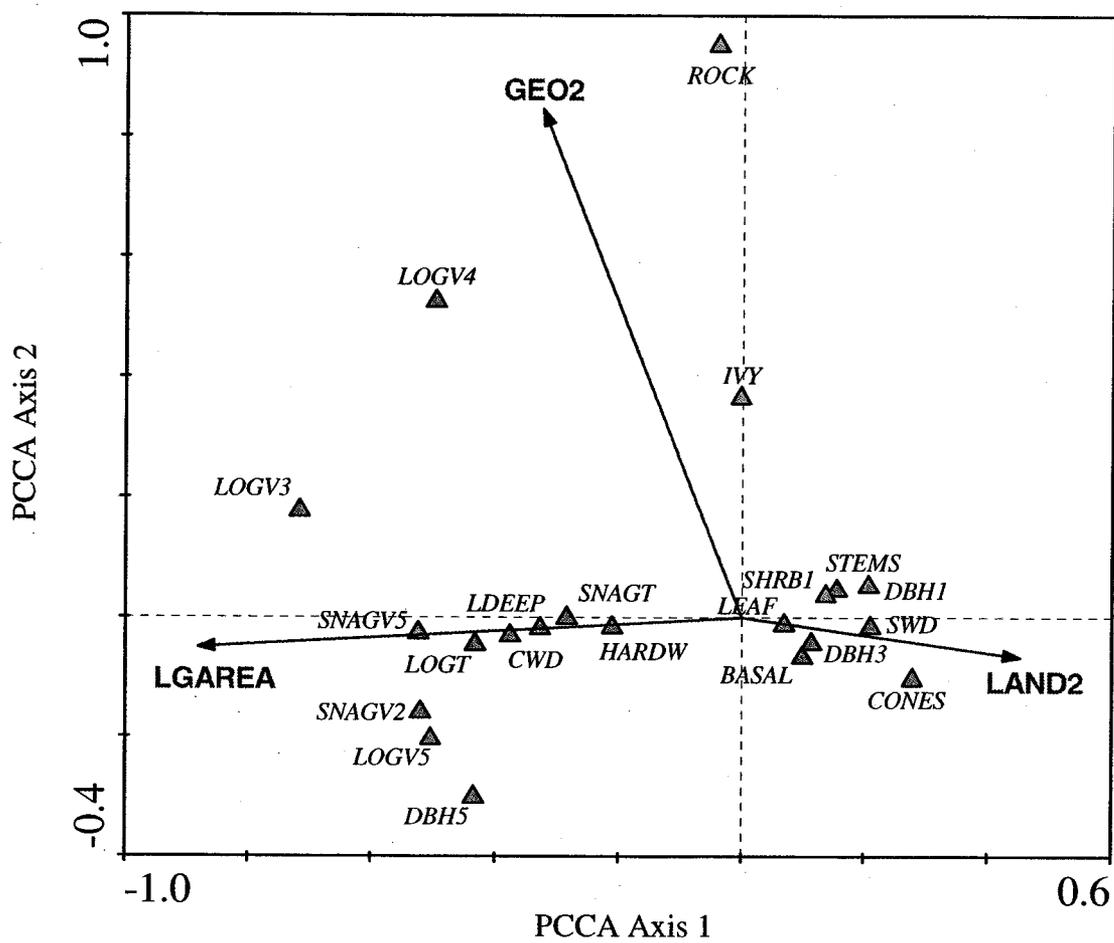


Fig. 2-4

CHAPTER 3: RICHNESS AND COMPOSITION OF PACIFIC NORTHWEST  
MAMMAL COMMUNITIES FRAGMENTED BY DEVELOPMENT: EFFECTS OF  
LOCAL HABITAT, PATCH STRUCTURE, AND THE URBAN MATRIX

**Abstract**

Urban development is a major contributor to habitat loss and fragmentation in North America, and results in the degradation of habitat remnants within cities. However, the effects of these changes on local wildlife communities remain largely unknown. We used multiple regression, nested subset analysis, and non-metric multidimensional scaling to test the effects of habitat degradation, patch characteristics (size and isolation of fragments), and landscape composition on the richness and composition of small mammal communities in forest fragments in the greater Portland, Oregon metropolitan area. Smaller fragments were more isolated, occurred in more urban matrices, and contained more degraded habitat. After rarefaction, regressions of species richness showed that native mammals declined in patches that contained fewer wetlands and streams or were smaller and occupied more urbanized landscapes. In addition, native richness increased with greater canopy tree coverage in the developed neighborhoods around forest patches. Insectivores were more restricted in their distribution than native rodents, and correlated with local forest structure, including higher volumes of coarse woody debris and deeper organic litter layers. Non-native species richness increased in small patches in more urbanized landscapes.

Both native and non-native rodents were significantly nested, but insectivores were not. The results indicate that small mammals in Pacific Northwest forests experience significant local extinctions as a result of urban fragmentation, possibly through a combination of patch isolation and edge-related habitat degradation. However, multicollinearity between environmental variables made it impossible to identify causal mechanisms with certainty. The sequence of species loss had no relationship to home range or body size; niche breadth and ability to move through the matrix probably determine the tolerance of small mammals for urbanization.

### **Introduction**

Human actions differ from historical disturbance regimes in their effects on wildlife habitat quality (Lawlor 2003) and in the spatial and temporal scales of their impacts (Martin and McComb 2003). As a result, anthropogenic habitat modification has contributed to population declines and extinction in numerous species worldwide, primarily through habitat loss and fragmentation (Fahrig and Merriam 1994). By far the most intense and widespread human disturbances occur in conjunction with land transformation, particularly agricultural conversion and urbanization (Vitousek *et al.* 1997). Such activities affect nutrient cycling (Weathers *et al.* 2001, Vasconcelos and Luizao 2004), succession (Robinson *et al.* 1992, Laurance *et al.* 1998, Yao *et al.* 1999), susceptibility to exotic invasion (Smallwood 1994), habitat structure and microclimate (Chen *et al.* 1995, Laurance *et al.* 1997), disease spread (Deem *et al.* 2001), competitive interactions (Songer *et al.* 1997, Nupp and Swihart 2001), and

predator-prey relationships (Crooks and Soule 1999, Crooks 2002). Where anthropogenic disturbances are sufficiently intense, changes may lead to long term alterations of remnant habitats, possibly preventing their natural regeneration for the foreseeable future (Lomolino and Perault 2000).

The response of wildlife communities to anthropogenic landscape change can be complex and depends not only on the scale, type, and intensity of the disturbance, but also on the species' natural histories (Swihart *et al.* 2003). The occurrence or abundance of a species in the patch depends fundamentally on the suitability of the local habitat (Hutchinson 1957, Brown and Kodric-Brown 1977). Within a single stand or patch, individual habitat elements may be utilized as cover from predators, forage, denning sites, or may provide favorable microclimates. Local disturbances (e.g. trampling, removal of coarse woody debris) may reduce the availability of important resources. As a result, populations may decline, the habitat may become a sink (Pulliam 1988), or it may become usable only for dispersal. More intense disturbances (e.g. agricultural or housing development) may render the habitat unusable by some species, resulting in complete habitat loss and providing an effective barrier to dispersal (e.g. Mills 1995, Bolger *et al.* 1997, Goheen *et al.* 2003). High proportions of intense disturbance across the landscape result in habitat fragmentation (i.e. the reduction and geographic separation of individual habitat patches; Martin and McComb 2003).

Habitat fragmentation increases the influence of edges effects on remnant patches, which can exacerbate and accelerate declines in habitat quality within the

patches (Matlack 1993, Fahrig and Merriam 1994, Laurance 1994, Mills 1995, Collinge 1996, Laurance *et al.* 1997). It may also affect local populations through mechanisms that are unrelated to local habitat quality. Theoretically, as fragments decline in area and populations become smaller, the risk of local extinction due to stochastic demographic or environmental events increases (McArthur and Wilson 1967, Hanski 1999). With greater patch isolation, the probability of recolonization or rescue by dispersers from other populations declines (Brown and Kodric-Brown 1977). In practice, patch characteristics such as area and isolation become important only when habitat availability is reduced to 20 – 30% of its original space (Andr n 1994). In such scenarios, a species' tolerance of the matrix (the landscape separating remnant habitat fragments) can strongly influence its prevalence across the landscape (Laurance 1991, Gascon *et al.* 1999b). As a corollary, if the matrix is heterogeneous and includes different levels of disturbance, fragments surrounded by less hostile landscapes (that is, landscapes containing high proportions of moderately usable or easily traversed habitats) may contain more species (Gascon *et al.* 1999b, Ricketts 2001).

In this context, urban development may be viewed as a conjoined suite of disturbances, occurring across a range of temporal and spatial scales. Outright habitat loss and fragmentation may be the most prominent of these effects, but they also include habitat degradation within remnants due to trampling and stem breakage (Matlack 1993, Malmivaara *et al.* 2002), chemical pollution and climatic changes (Pickett *et al.* 2001), and invasion by human associated competitors and predators

such as rats (*Rattus spp.*) and house cats (*Felis catus*) (VanDruff and Rowse 1986, Bolger *et al.* 1997, Crooks and Soule 1999, Crooks 2002). For some species, roads and developed areas may present significant barriers to dispersal, resulting in the effective isolation of habitat remnants (Forman and Alexander 1998). As a consequence, cities may experience very high local extinction rates, even in patches of relatively intact habitat (VanDruff and Rowse 1986, Dickman 1987, Bolger *et al.* 1997, How and Dell 2000, McKinney 2002).

The existence of numerous natural forest fragments in the city of Portland, Oregon (U.S.A.) gave us the opportunity to conduct a natural experiment to evaluate the impacts of urbanization on small mammal communities in Pacific Northwest forests. With a few exceptions (e.g. the western red-backed vole, *Clethrionomys californicus*, Mills 1995), many small mammals in this region have relatively broad niches and significant tolerance for disturbance (Verts and Carraway 1998, Hallett *et al.* 2003, Smith *et al.* 2003). However, declining capture rates or abundances in some locations have raised concerns that even this disturbance adapted community may be unable to adjust to anthropogenic habitat changes (Lawlor 2003). Most research concerning the effects of landscape change and forest fragmentation on Pacific Northwest wildlife has occurred in the context of timber harvest (e.g. Rosenberg and Raphael 1986, McGarigal and McComb 1995, Lomolino and Perault 2000, Lomolino and Perault 2001, Martin and McComb 2002), but positive correlations between human population density and forest fragmentation in this region suggest that urbanization should be of at least equal concern (Butler *et al.* 2004). Nonetheless, no

studies have yet examined the potential impacts of urban development on Northwest mammal communities.

We observed differences in small mammal species richness and composition in forest fragments in the greater Portland metropolitan area, and used a patch based analysis to relate mammal communities to variation in habitat structure, patch characteristics, and surrounding landscape composition. Stepwise multiple regression was used to relate species richness to environmental changes. In addition, we examined changes in nestedness and composition among subsets of the small mammal community, hypothesizing that particular groups of species (e.g. native rodents, non-native rodents, insectivores) may respond differently to urbanization. In particular, we expected native species to decline as landscapes became more urbanized and fragmented and local habitats became more disturbed. We also predicted that insectivores, with their lower vagility and greater susceptibility to microclimatic changes, would respond more strongly than native rodents. We expected non-native species to increase in response to landscape urbanization and patch disturbance, as predicted by their affinity with anthropogenically modified habitats.

## **Methods**

### *Study Location*

The greater Portland metropolitan area (approximately 45°31' N, 122°40' W) lies at the confluence of the Willamette and Columbia rivers in northwest Oregon. It spans the mouth of the Willamette Valley, as well as the Tualatin Mountains, a spur of

the Oregon Coast Range that forms the valley's western boundary. Our study was located in this western portion of the city, in an area that has undergone only relatively recent urbanization (beginning 75 – 100 years ago). Due to the steep slopes and significant land use and conservation planning on the part of local and state governments (Metro 2002, Baker *et al.* 2004), this portion of the city has retained a substantial proportion of natural forest cover (ca. 30%). However, the native landscape has been heavily divided and fragmented by roads and development, resulting in an archipelago of forest patches, connected to varying degrees by riparian corridors and canopy cover over developed areas (Fig. 3-1). Elevations in our study area range from approximately 40 m to 260 m.

The climate in this region is mild, with warm, dry summers and cool, wet winters with only infrequent snowfall. Temperatures and precipitation average 11.8°C and 94.2 cm per year (30 year norms, Taylor and Hannan 1999). Douglas fir (*Pseudotsuga menziesii*) and big-leaf maple (*Acer macrophyllum*) dominate the tree canopy, although western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), and European sour cherry (*Prunus cerasus*) are also common. In addition, lower elevation sites include Oregon white oak (*Quercus garryana*) and Oregon ash (*Fraxinus latifolia*). Understories vary more widely than tree communities, and include western sword fern (*Polystichum munitum*), Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), California hazelnut (*Corylus cornuta*), vine maple (*Acer circinatum*) and various *Rubus spp.* Two invasive non-native shrubs, English ivy (*Hedera helix*) and Himalayan blackberry (*Rubus discolor*)

are also widespread, and sometimes exclude other understory plants. Detailed discussions of plant community composition, forest structure, and landscape composition, as well as vegetation survey techniques and landscape analyses, may be found in Chapter 2.

The 25 patches selected for this study represent a subset of 48 sites used in Lichti (Chapter 2) and Bailey (*unpublished*), and lay mostly in the Tualatin Mountains (Fig. 3-1; throughout this paper, the terms site, patch, and fragment are used interchangeably). Four sites occupied the Tualatin River valley, to the southwest of the hills. All of the patches were publicly accessible, consisted of second growth forest with relatively closed canopies (> 55% cover, most > 70%), ranged in area from 0.3 ha to 1538 ha, and were isolated to various degrees by urban development. Patches consisted of natural forest with intact flora in all vertical strata. Their edges were delineated on the basis of publicly accessible roads or development using a combination of geographic information system (GIS) coverages and site visits (Chapter 2). We assumed that development and roads presented significant barriers to small mammal movements. While the presence of canopy cover outside of patches may invalidate our definition from some species' perspectives (e.g. fox squirrels, *Sciurus niger*), we favored a physical definition because data on small mammal movements in relation to apparent boundaries in this system were lacking, and because it lended itself more easily to interpretation in terms of management.

*Small Mammal Surveys*

We conducted live-trapping surveys from May through September in 2002 and 2003. Thirteen sites were sampled in the first year, and 17 in the second. Eleven sites were sampled in both years. Each site contained from 1 to 10 line transects, depending on the size of the patch. Unless constrained by the patch's area or shape, transects were 160 m long and randomly located. In sites smaller than 3.7 ha in area, transects were located arbitrarily to maximize the number of traps that could be placed in the fragment. No transect was less than 50 m long. Trap stations were established at 10 m intervals along the transects. Each station received 2 Sherman live traps (7.5 x 9.0 x 30 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida), baited with whole oats and provisioned with polyester batting for insulation. Traps were located within 2 m of a station, and took advantage of natural cover, logs, and runways to maximize capture probabilities. To minimize theft and vandalism, as well as risk to captured animals, traps were also positioned to avoid visibility from any nearby trails. Half of the 2002 transects and all of the 2003 transects also received a single Tomahawk trap (15 x 15 x 60 cm; Tomahawk Live Trap Company, Tomahawk, Wisconsin) at every fifth station (i.e. 40 m intervals). Tomahawks were baited with a combination of whole oats and raw peanuts or peanut butter, and were placed within 5 m of the station center.

Each transect was visited only once during the 2 year study, for a period of four days and nights. Because we were surveying for both diurnal and nocturnal species, traps remained open around the clock and were checked twice daily, at dawn

and dusk. Captured animals were identified to species, sexed, weighed, and individually marked with numbered Monel™ ear tags (National Band and Tag Company, Newport, Kentucky). Shrews (*Sorex spp.*) and shrew moles (*Neurotrichus gibbsii*) were marked with a permanent marker instead of ear tags. Relative abundance was estimated as the minimum number of unique individuals. For sites that were surveyed in both years, the maximum number of individuals detected in a given year was used for rarefaction (see below).

In addition to trapping, 1-6 point count stations were established in each patch to detect diurnal squirrels. Stations had a 50 m fixed radius and were separated by a minimum of 150 m, but were otherwise randomly located. Each station was visited 3 times from May to July, 2003, for 10 minutes per visit. Both auditory and visual detections were recorded. The number of squirrels in the patch was taken as the maximum number of individuals detected during any one visit. Because it was impossible to determine whether squirrels detected during point counts had also been trapped, we used the maximum number of individuals detected in each patch using either trapping or point counts for the purposes of rarefaction. Detailed point count protocols may be found in Bailey (*unpublished*). The sequences of site visits for both trapping and point counts were randomized over the season.

### *Environmental Variables*

#### *Habitat Characteristics*

We quantified floristic and structural attributes of forests at 180 points across the 25 study sites, with 2 to 16 points per site. As with the mammals, more samples were taken in larger fragments in an attempt to capture the potentially greater variation in microhabitats at these sites (Dunstan and Fox 1996). At each point, vegetation was sampled within a 10 m radius circular plot, quartered by two 20 m transects. Within the circle, we identified to species and measured the diameter breast height (DBH) of all woody stems  $\geq 2.5$  cm DBH. All logs and snags  $\geq 10$  cm diameter (DBH for snags, widest part for logs) were also counted, and were assigned to one of five decay classes (Cline *et al.* 1980, Sollins 1982). Ground layer variables were quantified by laying a meter-stick perpendicular to each transect at 2 meter intervals. The percent cover of herbs (both grasses and forbs), moss, bare mineral soil, and woody debris (2.5 – 10 cm) was estimated as the fraction of stations in which the meter stick contacted each cover type. The depth of the organic litter layer was also recorded at each station, and averaged for the plot. Percent shrub cover was similarly estimated by recording the number of transect stations with stem or leaf hits on a 3 m long, 3 cm diameter vertical pole, divided into three layers (low: 0.0 to  $< 0.5$  m, medium: 0.5 to  $< 1.5$  m, high: 1.5 to  $< 3$  m). Canopy closure was estimated at each station using a 3 cm diameter ocular tube, and averaged for the plot. To provide a measure of the intensity of human disturbance, we estimated the distance from the center of each plot to the nearest trail. All habitat variables were averaged across plots at each site. We also recorded the

universal transverse mercator (UTM) coordinates of each vegetation sample point to  $\pm$  10 m, using a Garmin 12 XL GPS unit (Garmin International, Olathe, Kansas). The centroid of these measurements for each site was used to test for spatial patterns during regression analyses.

We estimated the elevation of each vegetation plot using a 2.0 m digital elevation model of the Portland metropolitan region (DEM, Metro 2004), and recorded the range of elevations surveyed at each site as an estimate of overall slope. We also calculated the density of permanent streams and wetlands in each fragment from GIS data (Metro 2004). Detailed accounts of our habitat methodology and structural and floristic variation among our sites are available in Chapter 2.

### *Landscape Variables*

We used GIS coverages prepared from 2001 aerial photos and municipal land use records (Metro 2004) to assess landscape composition in a 1 km buffer around each site, and to measure the size, shape, and geographical isolation of each study fragment (Chapter 2). A categorical land use map was created in ArcGIS 8.2 (ESRI 1999) differentiating forest, developed areas with canopy cover, residential areas without visible canopy cover on 3.05 m (10 ft) resolution aerial photos, treeless open spaces, and commercial-industrial areas. Agricultural fields, open water, and unclassified land uses were also present, but had highly skewed distributions and were excluded from analyses. Developed canopy was defined as any location showing canopy cover on aerial photos, but for which tax records showed that substantial

building development had occurred on the ground (see Chapter 2). Treeless open spaces were defined as areas classified as public property, rural, or vacant in the GIS database (Metro 2004), and which lacked visible canopy cover on aerial photos.

The program FRAGSTATS (McGarigal and Marks 1995) was used to determine the percentage of each land use category in the buffer. In addition, we calculated the *AREA* and *SHAPE* of each study fragment. The *SHAPE* index, which provides a measure of patch complexity, increases as patch edges become more convoluted. Unlike simple perimeter-to-area ratio, it is not necessarily correlated with patch area (McGarigal and Marks 1995). In addition, we calculated the mean proximity index (*MNPROX*) of all forest patches in the 1 km buffer. The proximity index measures the connectedness of a focal patch as the sum of the area-weighted distances to all other patches of a similar type within a given search radius (1 km in our analyses, Gustafson and Parker 1992). It increases as patches become less isolated. By calculating the mean proximity of all forest patches in the landscape, we obtained a measure of overall landscape connectivity. Previous analyses showed that this measure correlated with the proximity of individual study fragments (Chapter 2). Both *AREA* and *MNPROX* were log-transformed before use.

### *Statistical Analyses*

Principal components analysis (PCA) was used to summarize variation in local forest structure, patch geomorphology, and landscape composition. By using separate PCA axes to describe discrete habitat gradients (i.e. forest structure, geomorphology,

and landscape structure), we avoided problems associated with small sample size, produced readily interpretable axes, and sought to separate different components of the environment in subsequent analyses. We used axes for geomorphic and landscape variables developed in a previous study to facilitate comparisons between this and other studies (Chapter 2). To quantify forest structure, we selected specific characteristics on the basis of *a priori* expectations of their relevance to small mammals (see Table 3-1, Verts and Carraway 1998, Hallett *et al.* 2003, Smith *et al.* 2003). We checked the normality of these variables using a Kolmogorov-Smirnov goodness-of-fit test and *z*-transformed them to fit a standard normal distribution (Zar 1999) before entering them into the PCA. Axes were retained according to the broken-stick criterion (Frontier 1976), and interpreted by examining correlations between the axes and forest structure variables.

Because sampling effort was uneven between sites and correlated with patch size, analysis of simple species richness might lead to spurious conclusions. To correct for this, we calculated expected species richness using rarefaction (Hayek and Buzas 1996). Given count data for each site, this technique calculates the number of species that one would expect to encounter at a site, given a standard sample size (i.e. number of individuals). Comparisons between sites are usually made by setting the rarefacted sample size ( $n_r$ ) equal to the number of individuals detected at the least sampled site. Only 3 individuals were caught at one of our sites. However, as  $n_r$  approaches 1, patterns in the data become more muted, and the probability of masking real effects increases. After preliminary analyses, we set  $n_r = 5$  and assumed that had

we captured 2 more individuals at this site, they would not have represented new species. Given the overwhelming dominance of deer mice (*Peromyscus maniculatus*) across our samples, this is probably a safe assumption (see Results and Chapter 4).

Rarefaction was performed separately for all species, native species, native rodents, and non-native rodents using Primer 5.2.9 (Clarke 1993). Counts of individuals for each species at each site were taken as the maximum of the number trapped in a given year or detected by point count. Because very few insectivores and non-native rodents were detected overall, and several sites lacked them completely, their expected richness was calculated as the difference between expected overall richness and expected richness with these species excluded.

We used multiple regression to identify possible determinants of expected mammal richness in Portland forests. Analyses were conducted using a stepwise selection process, in which all of the independent variables were entered together ( $\alpha = 0.05$  to enter, 0.10 to exit). Before conducting these analyses, we tested for any underlying spatial structure in the mammal data by conducting a trend surface analysis using the third order polynomial of the patches' UTM coordinates (Borcard *et al.* 1992). Although we were not interested in spatial patterns, they could confound subsequent analyses if both species richness and environmental variables correlated with an underlying spatial gradient. Space was therefore treated as a nuisance variable and partialled out if it was significant (Borcard *et al.* 1992, Fortin and Gurevitch 2001).

We studied patterns of community assembly (or disassembly) using the nestedness temperature calculator (Atmar and Patterson 1993, 1995). Habitat patches

are considered to be nested if they show a triangular pattern of species occurrence when ranked according to species richness, so that successively less diverse assemblages represent subsets of all more diverse patches. Such a pattern implies that species are lost or gained according to some underlying causal mechanism, rather than at random. Given a presence-absence matrix, the calculator determines a system-wide index of nestedness,  $T$ , which varies from  $0^\circ$  in a perfectly nested system to  $100^\circ$  for a completely random matrix (Atmar and Patterson 1993). The statistical significance of  $T$  is then calculated by Monte Carlo permutation ( $n = 50$ ). In addition, individual temperatures are calculated for each species. If an overall pattern of nestedness occurs, species that do not follow that pattern are termed idiosyncratic, and their individual temperatures will be higher than the overall  $T$ . To test the hypothesis that groups of small mammals assembled separately according to their natural history, we calculated  $T$  for 5 different matrices: all species, native species only, insectivores, native rodents, and non-native rodents.

To check for effects of passive sampling on nestedness patterns, we compared the average number of species trapped on individual transects in each site to the richness of the site as a whole using Pearson correlation. A significant positive relationship indicated that more species were found in equivalently sized portions of species-rich sites than species-poor sites, and therefore showed that observed nestedness patterns probably did not arise from passive sampling. We also tested the hypotheses that native species nested according to body size or minimum spatial requirements. This was done by using Spearman rank correlation to compare actual

extinction order, expressed as the number of sites occupied, to the expected orders given average adult body mass (from our field data) or published home range sizes for western Oregon (Harris 1984). The relationship between native and non-native richness was also compared, using Pearson correlation.

Finally, to provide insight into the response of individual species to environmental variation in Portland forests, we employed non-metric multidimensional scaling (NMDS) to provide a 2-dimensional ordination of the study sites on the basis of community composition. We chose Bray-Curtis distance, an ecologically meaningful metric appropriate for binary data (Legendre and Legendre 1983), to quantify site dissimilarity. After partialing out spatial patterns (Borcard *et al.* 1992), the NMDS axes were compared to environmental PCA axes using Pearson correlation. NMDS was performed using Primer; all other analyses were carried out in SPSS 11.5 (SPSS 2002).

## Results

A total of 2146 individual animals were detected in 27,372 trap opportunities and 261 point count visits (2018 trapped, 128 point count detections), representing 14 species (10 native, 4 non-native). Unrarefied species richness ranged from 1-9 species per patch, with 1-8 natives and 0-3 non-natives. Deer mice (*P. maniculatus*) dominated captures in all locations, with 72.1% of the overall detections. Townsend's chipmunks (*Tamias townsendii*, 11.5%) were also common. Other species included Douglas squirrels (*Tamiasciurus douglasii*, 4.5%), fox squirrels (*Sciurus niger*, 3.3%),

Trowbridge's shrew (*Sorex trowbridgii*, 2.9%), creeping voles (*Microtus oregoni*, 1.3%), Norway rats (*Rattus norvegicus*, 1.2%), and vagrant shrews (*S. vagrans*, 1.1%). American shrew-moles (*Neurotrichus gibbsii*), short-tailed weasels (*Mustela erminea*), eastern grey squirrels (*S. carolinensis*), western grey squirrels (*S. griseus*), northern flying squirrels (*Glaucomys sabrinus*), and black rats (*R. rattus*), each represented less than 1% of detections.

### *Principal Components Analyses*

Table 3-1 presents correlation coefficients for individual forest structural variables. The first three habitat axes extracted from the PCA on local forest structure explained a total of 60.1% of the variation among sites (Table 3-2). The first axis (*HABI*) correlated positively with most measures of coarse woody debris, including the total number of logs and snags, the number large logs (> 20 cm diameter), the total number of heavily decayed logs and snags (class 4 and 5), and the total volume of coarse woody debris. It also showed a strong positive correlation with the diversity of coniferous tree species, and somewhat less strong relationship with the depth of the organic litter layer, the number of large snags, mid-level shrub cover (0.5-1.5 m, e.g. western sword fern, Oregon grape) and average distance to the nearest trail from vegetation sample plots (i.e. inversely related to trail density). *HABI* was negatively correlated with cover of low shrubs (0.0-0.5 m, e.g. English ivy). In general, sites with high scores on this axis were most similar in habitat to what would be

encountered in more mature, unmanaged second-growth forests in the Oregon Coast Range.

The second habitat axis (*HAB2*) was associated with shrub cover above 1.5 m, and high frequencies of moss and large woody debris (2.5 – 10 cm diameter) on the ground (Table 3-2). High scoring sites had a higher diversity of angiosperms among their tree communities, and generally had high total stem counts, indicating the presence of many small trees and large shrubs (e.g. California hazelnut, vine maple). These sites also tended to have more herb cover and bare mineral soil, although these correlations were less strong. Total basal area, the number of trees > 30 cm DBH, litter depth, and the percentage of conifers in the community were negatively associated with this axis (Table 3-2). *HAB3* was associated with bare soil, low shrubs, low stem densities, and large, relatively young snags (Table 3-2).

Correlations between specific variables and the landscape and geographic axes for sites in this study are shown in Table 3-3. *GEO1* described a gradient of increasingly complex terrain, with higher mean elevations and local (i.e. vegetation plot-scale) slopes, greater vertical relief, and more incised terrain with more streams. Not surprisingly, wetland density correlated negatively with this axis. However, wetlands were positively related to *GEO2*, which was also associated with lower elevations. *LAND1* covered a broad landscape urbanization gradient, running from relatively unfragmented, high-forest landscapes to less inter-connected heavily developed landscapes with high densities of streets, buildings, and people. These sites also had large amounts of residential land use in their buffers. *LAND2* was also

negatively associated with forest cover, but primarily described presence of large trees in the matrix around patches. It ran from areas of development covered by an intact canopy but disturbed understory, to treeless open spaces such as school yards and playing fields. Often, these land uses were clustered around forest patches (Chapter 2).

Significant correlations existed between several sets of environmental gradients (i.e. PCA axes; Table 3-4). In particular, patch area correlated with *HABI*, *GEO1*, *LAND1* and *SHAPE*. These four variables were also intercorrelated among themselves. As a consequence, multicollinearity presented a problem in regression analyses, and should be kept in mind while interpreting these results.

### *Species Richness*

After rarefaction, trend surface analyses showed no significant relationships between spatial variables and richness for any set of small mammals. Table 3-5 presents the results of stepwise regression models. Total expected species richness (hereafter, richness) ranged from 1.00 to 2.63. Overall richness increased with *GEO2* and decreased with *LAND2*. More species were found in patches with high water availability and more canopy cover in the matrix. Native species richness showed similar patterns, but also decreased with *LAND1*, demonstrating that fewer native mammal species were found in more urbanized landscapes that lacked forest cover and connectivity. Insectivores correlated positively with *SHAPE*, but no other variable, suggesting that their richness increased as patches became more convoluted.

The response of native rodents was qualitatively identical to that seen in overall richness, with increased numbers of species in wet patches surrounded by high proportions of canopy cover in the matrix. Non-native rodents, on the other hand, increased in richness with *LANDI*, showing a positive correlation with urban development.

Native and non-native richness were not significantly correlated ( $r = -0.220$ ,  $P = 0.290$ ). However, examination of scatter plots revealed that this was due to the absence of non-native species from the two smallest sites. With these high-leverage points removed, the relationship became significant ( $r = -0.499$ ,  $P = 0.015$ ).

### *Nestedness*

The nestedness temperature calculator indicated that the overall small mammal community in Portland forest fragments was significantly nested (Table 3-6, see also Fig. 5). However, the temperature calculator does not provide conservative estimates of the statistical significance of  $T$ , so  $P$ -values should be treated with caution (Fischer and Lindenmayer 2002). More useful information may be gained by examining the actual nestedness structure of the community, including individual temperatures. In general, if all species are responding consistently to a single gradient (e.g. faunal relaxation due to selective extinction in land-bridge islands), there should be few idiosyncratic species (i.e. species with high individual temperatures), even at relatively low system temperatures (Atmar and Patterson 1993). On the other hand, if different segments of the community have assembled along separate gradients, or responded

oppositely to the same gradient (e.g. extinction mixed with invasion), this should be apparent in the identities and natural histories of the non-conformist species.

Our data showed that half of the species had individual temperatures equal to or greater than the overall system temperature of 15.69°. These included all of the non-native species, as well as two of the three insectivores. Splitting the community to test the hypothesis that small mammals responded differently, depending on their origin and taxonomy, we found that the native community as a whole was only moderately more nested than the complete mammal fauna (Table 3-6). However, when insectivores, native rodents, and non-native rodents were examined separately, we found that both native and non-native rodents showed highly nested patterns of occurrence, with temperatures  $< 3^\circ$  in both cases. Insectivores were not significantly nested (Table 3-6, Fig 5b). Species with small home ranges were no less likely to become extinct than species with large home ranges (Spearman correlation:  $\rho = 0.248$ ,  $P = 0.489$ ), and body size did not correlate with extinction risk (Spearman correlation:  $\rho = 0.377$ ,  $P = 0.461$ ). Nested patterns probably did not arise as a result of passive sampling, as more species were captured on individual transects in more species-rich sites (Pearson correlation:  $r = 0.421$ ,  $P = 0.045$ ).

#### *NMDS of Small Mammals*

Fig. 5 shows a 2-dimensional NMDS plot for small mammal communities in Portland forests. After controlling for spatial variation, the first axis correlated significantly with *HABI* ( $r = -0.594$ ,  $P = 0.004$ ), *GEO2* ( $r = -0.613$ ,  $P = 0.002$ ), and

*LGAREA* ( $r = -0.604$ ,  $P = 0.003$ ). The second axis had no spatial component, and correlated with *HABI* ( $r = -0.526$ ,  $P = 0.008$ ), *GEOI* ( $r = -0.583$ ,  $P = 0.002$ ), *LANDI* ( $r = 0.619$ ,  $P = 0.001$ ), *LGAREA* ( $r = -0.539$ ,  $P = 0.005$ ), *LGPROX* ( $r = -0.521$ ,  $P < 0.008$ ), and *SHAPE* ( $r = -0.513$ ,  $P < 0.009$ ). Thus, points in the lower left corner of the plot represented relatively mature, undisturbed, mesic sites in rougher terrain. These fragments tended to be larger in area and better connected to surrounding forest. They also occupied less urbanized landscapes, and tended to have more complex shapes. Moving diagonally up and to the right, sites became more urban, smaller, more isolated, drier, and less mature in their forest structure. Native rodents nested to the left side of the plot (Fig. 5a), again demonstrating an affinity for mesic, mature forests with large amounts of coarse woody debris and diverse conifer communities. They also nested toward the bottom of the graph. Native insectivores and carnivores showed an even stronger, if somewhat less organized, association with the lower left corner (Fig. 5b). In contrast, non-native rodents clustered in the upper left corner (Fig. 5c), demonstrating an association with urbanization and a less intense attraction to mature forests, as shown by the negative correlation between *NMDS2* and *HABI*. However, like the natives, non-native rodents were also associated with wetlands. This was particularly true for the rats. Only deer mice occurred at all 25 sites.

## Discussion

Urbanization has become a major source of landscape fragmentation, contributing not only to the reduction and subdivision of remnant habitats, but also to

their degradation and invasion by non-native species (McKinney 2002). In the United States, developed landscapes cover 395,000 km<sup>2</sup> (Alig *et al.* 2004), and development has been identified as a leading cause of species endangerment (Czech *et al.* 2000). U.S. cities are expected to expand by as much as 79% over the next 25 years (Alig *et al.* 2004), and increasingly grow in decentralized patterns that maximize regional fragmentation and edge effects (Makse *et al.* 1995, Pickett *et al.* 2001). Globally, cities follow similar patterns. To address these issues, wildlife conservation must develop a better understanding of the ecological processes shaping animal communities in urbanized landscapes.

Our results indicate that fragmentation by urbanization has had a significant impact on small mammal communities in Portland forests. Overall species richness varied significantly among patches, and nested subset analysis revealed that community composition probably resulted from the interaction of at least two separate extinction-colonization processes. As landscapes became more urbanized and patches became smaller, drier, and more isolated, native small mammal communities became increasingly impoverished (Table 3-5, Fig. 3-2). Non-native mammals, however, gained richness in more urbanized settings with smaller, more disturbed forests. In addition, native rodents and insectivores may have responded differently to urbanization. Rodents increased in more mesic sites with high canopy cover in the surrounding matrix, while insectivores correlated most strongly with patch shape (Table 3-5) In the NMDS, insectivores were the most limited group, occurring mainly in larger, wetter, less degraded patches in less urbanized landscapes (Fig. 3-2).

Nested communities generally occur when individual species are deterministically lost (extinction) or gained (colonization) along some underlying environmental gradient (Patterson 1990). Small mammals have shown such non-random assembly under a wide range of circumstances (e.g. Cutler 1991, Laurance 1994, Gascon *et al.* 1999b, Lomolino and Perault 2000, Nupp and Swihart 2000), and for a variety of possible reasons, including direct area effects (Cox *et al.* 2004), differential dispersal ability (Goheen *et al.* 2003), and differential responses to local habitat alteration (Laurance 1994, Lomolino and Perault 2000). However, distinguishing between potential causes of nestedness can be difficult when environmental gradients correlate with each other. Because anthropogenic landscape alteration modifies many ecological processes (Vitousek *et al.* 1997), this is often the case in fragmented systems. Interpretation can be further complicated by interactions between factors that influence community composition (Dunstan and Fox 1996). In addition, the effects of landscape patterns are not always consistent across taxa (Robinson *et al.* 1992).

In Portland less urbanized landscapes (low *LANDI*) were associated with larger patches, less degraded forest structure, and more complex terrain (Table 3-4). This pattern probably resulted from a tendency to avoid construction on steep hillsides or ravines, leaving these locations relatively undisturbed. In addition, edge related anthropogenic disturbances are presumably higher in smaller, more urban forest fragments, resulting in greater habitat degradation in these sites (Matlack 1993, Malmivaara *et al.* 2002). Recreational users may also be more likely to create new

paths in terrain with less relief and in small, neighborhood woodlots than in larger parks with maintained trail systems. A similar phenomenon may have occurred with wetlands. Wetland density in our sites was also associated with high frequencies of native forest herbs, as opposed to disturbance associated exotics (Chapter 2).

Given the correlations between different habitat gradients in Portland (i.e. forest structure, patch size, patch isolation, geomorphology, and landscape composition), we cannot conclusively determine the causes of nestedness or species extinctions in this system. However, our results suggest that community composition was determined by habitat differences or differential, species-specific isolation, rather than by area effects *per se* (McArthur and Wilson 1967).

Recent studies have indicated that traditional island biogeographic factors (i.e. patch area, geographic isolation) may play only a limited, indirect role in shaping terrestrial small mammal communities (Doak and Mills 1994, Lomolino and Perault 2001, Martin and McComb 2003). Despite significant species-area effects, Nupp and Swihart (2000) found no correlation between body size and sensitivity to fragmentation in rodents occupying Midwestern hardwood forests. Larger mammals were also no more likely than smaller ones to become extinct in fragmented Australian rainforests, indicating that neither minimum area requirements nor potential vagility in unfragmented habitats is necessarily a good predictor of sensitivity to fragmentation (Laurance 1991, but see Cox *et al.* 2004). We likewise found no relationship between extinction risk and species' body sizes or home ranges. Thus, although some species may have been excluded from smaller sites as a consequence of area requirements

(Cox *et al.* 2004), this does not appear to have driven the overall relaxation of native small mammal fauna in Portland forest fragments.

While we did not examine it directly, species' abundances in exurban landscapes also appear unable to predict extinction risk. Some normally abundant species such as deer mice and Townsend's chipmunks were widespread, but others that are commonly encountered outside of the city were largely absent. Creeping voles, for example, are an abundant species in the Oregon Coast Range (e.g. McComb *et al.* 1993, Carey and Wilson 2001, Suzuki and Hayes 2003), but were apparently negatively affected by urban fragmentation. This contrasts with the results of Bolger *et al.* (1997), who showed that initially abundant coastal sage scrub species were more resistant to extinction in California.

Several authors have concluded that niche breadth and dispersal ability appear to largely determine persistence in fragmented and disturbed landscapes (Laurance 1991, 1994, Gascon *et al.* 1999b, Nupp and Swihart 2000, Ricketts 2001, Goheen *et al.* 2003, Swihart *et al.* 2003). Our results support this hypothesis. Mammals of western coniferous forests tend to be generalists (Lawlor 2003), and the most frequent species in our surveys were generalist terrestrial rodents (e.g. deer mice, chipmunks), tree squirrels, and Trowbridge's shrew, probably the most widespread generalist insectivore in western Oregon (Verts and Carraway 1998). Relatively specialized species, such as western red-backed voles, Baird's shrews (*S. bairdi*), marsh shrews (*S. bendirii*), and Pacific jumping mice (*Zapus trinotatus*) were not detected, and have

not been captured in pitfalls or trap-webs operated by other researchers in these fragments (pers. comm. L. Roberts, L. Dizney).

The prevalence of non-native species in more urbanized sites in Portland reinforces this conclusion. These fragments tended to be smaller, more isolated, and more disturbed than fragments containing rich native mammal communities. All of the non-natives species that we detected are found in the urban matrix (pers. observ.), and most likely invaded fragments from the surrounding neighborhoods. Similar patterns have been observed in a variety of situations, including rural forest fragments in Australia (Dunstan and Fox 1996) and Madagascar (Ganzhorn 2003), and urban habitat fragments in North America (VanDruff and Rowse 1986, Bolger *et al.* 1997). Although inverse correlations between native and non-native species have been noted, there has been little evidence that direct competitive interactions influence species richness or composition in most of these studies (but see VanDruff and Rowse 1986). Instead, it appears that non-native species may passively replace natives as a function of their tolerance for matrix habitats (Laurance 1991, 1994, Gascon *et al.* 1999b).

Urban development has the potential to effectively isolate remnant mammal populations. Bolger *et al.* (1997), for example, found that despite significant species-area effects, the distance between coastal sage scrub fragments had no effect on native mammal richness. They interpreted this to mean that fragments in their study were completely isolated and undergoing faunal relaxation. In Portland, native small mammal richness declined with increased urbanization and patch isolation, possibly indicating that for these species, developed landscapes presented an impediment to

dispersal, but not an absolute barrier. Given the correlations among landscape composition, patch area, and forest structure in our dataset, this conclusion must be treated as tentative. However, it receives some support from the positive correlation between native species richness and canopy cover in the matrix.

If the matrix acts as a selective filter, rather than an absolute barrier, sites surrounded by more permeable matrices should contain greater numbers of species (Gascon *et al.* 1999b). In addition, tolerance for the matrix often plays a large part in determining which species successfully exploit fragmented landscapes (Laurance 1991, Gascon *et al.* 1999b), and differential dispersal ability can result in nested community assembly among forest mammals (Nupp and Swihart 2000, Goheen *et al.* 2003). In Portland, canopy cover in the matrix surrounding forest fragments correlated positively with the richness of native rodents. The native rodents also displayed a highly nested pattern of assembly. Goheen *et al.* (2003) found that squirrels were more likely to cross agricultural fields during the growing season, when cover was more abundant. Canopy tree cover in the urban matrix may have a similar effect, particularly if tree retention is associated with landscaping that relies more heavily on shrubs rather than lawns. In addition, tree cover around fragments may facilitate movement between patches by providing a larger, more visible, or closer target for dispersers (Goheen *et al.* 2003). Matrix tree cover in Portland has also been associated with increased songbird abundance (Hennings and Edge 2003) and some native herbs (Chapter 2), suggesting that increasing urban canopy cover may be a relatively simple way of maintaining biodiversity in developed landscapes.

Native mammals in general, and native rodents in particular, also gained richness in more mesic sites (high *GEO2*, Table 3-5, Fig. 3-2). This was somewhat puzzling, considering that none of the native rodent species detected are closely associated with wetlands or riparian areas (Verts and Carraway 1998). In fact, creeping voles and Townsend's chipmunks were more abundant in upslope transects than in streamside transects in the Oregon Coast Range (McComb *et al.* 1993). These authors did capture more deer mice close to streams, but in the current study, deer mice were ubiquitous. Their prevalence among patches was unaffected by the availability of water.

More mesic sites in Portland were significantly correlated with the frequency of Oregon white oak (*Quercus garryana*,  $r = 0.488$ ,  $P < 0.05$ ) and salal (*Gaultheria shallon*;  $r = 0.361$ ,  $P < 0.05$ ), both of which could represent important food resources for small mammals. More mature, mesic Douglas fir forests in Oregon also contained a greater standing biomass of hypogeous fungal sporocarps than drier forests (Luoma *et al.* 1991). Ectomycorrhizal fungi constitute a significant portion of the diets of many Pacific Northwest small mammals (Hallett *et al.* 2003, Luoma *et al.* 2003, Smith *et al.* 2003). They are also the dominant source of nutrition for northern flying squirrels, our second most restricted species (Maser *et al.* 1985). It therefore appears likely that more mesic sites support more small mammals because they offer more food resources. In addition, if urbanization has effectively isolated forest fragments in the Portland region, the presence of wetlands at a site might buffer local habitat conditions against stochastic environmental variation. In particular, fragments

containing large quantities of available groundwater or many permanent streams might provide a more stable food supply in the event of drought.

Native insectivores were more severely affected by urbanization than were native rodents (Fig. 3-2). Although they were not significantly nested (Table 3-6), this may have resulted from their relatively low detectability in live-trapping surveys (Jones *et al.* 1996). Based on NMDS results, insectivores showed a strong association with larger, less disturbed forest fragments in less urbanized landscapes (Fig. 3-2). Despite the clear negative association with urbanization, however, the mechanisms underlying the loss of insectivores remain unclear. Species richness for this group was most closely associated with patch shape (Table 3-5, Fig. 3-5). The reasons for this association are unclear. Beetles were more abundant near developed edges in California (Bolger *et al.* 2000), so edges might provide a greater abundance of food. However, we have no data on arthropods to support this hypothesis. More complex patches were also positively associated with stream density ( $r = 0.532$ ,  $P < 0.001$ ; see Table 2-3), and with more mature forest structure, less urbanization, and larger patch sizes (Table 3-4). These factors might have contributed to insectivore richness. With their small body size and association with moisture (Verts and Carraway 1998), insectivores may have a more difficult time crossing built-up environments. If so, they might become isolated more easily than most rodents by barriers such as roads. In addition, downed logs and well developed litter layers, both of which were associated with mature forest conditions in our study, generally benefit insectivores. Decaying wood provides cover, nest sites, and invertebrate prey, and has been

positively associated with abundance and reproduction in Trowbridge's shrews and shrew-mole abundance (McComb 2003). Leaf litter may provide cover and foraging opportunities (Verts and Carraway 1998, Hallett *et al.* 2003).

## Conclusions

Fragmentation by urbanization has had significant negative effects on small mammal communities in Portland, resulting in substantial species loss. In contrast, industrial forest landscapes of western Oregon and Washington have experienced numerical declines of some species in response to fragmentation, but few outright extinctions (Rosenberg and Raphael 1986, Lomolino and Perault 2000, Lomolino and Perault 2001, Martin and McComb 2002, Lawlor 2003). This resilience probably arises from the community's evolution in a highly variable, frequently disturbed Pleistocene environment, which has led to the existence of a mammalian fauna that is somewhat tolerant of disturbance and able to recolonize successional patches once adequate habitat has been restored (Kirkland 1985, Lawlor 2003).

Given the significant effects of urbanization in this study, as well as the correlated effects of habitat degradation, urban forest patches in Portland will probably not recover their small mammal fauna naturally. In contrast to timber harvest, urbanization permanently alters the landscape between habitats, replacing it with a less permeable matrix that isolates forest remnants. Simultaneously, edge related habitat disturbances may help to maintain smaller patches in early seral stages (Chapter 2), which may reduce the ability of these fragments to support native species. This

combination of habitat degradation and isolation appears to have excluded all but the most generalist species from much of the urban landscape. Retention of trees in the developed matrix may help to facilitate movement by some species (e.g. squirrels). It may also mitigate the microclimatic effects of fragmentation on remnant forests (Chapter 2). However, until more is known concerning mammals' use of the matrix, specific responses to habitat disturbance, and the role of subsidized predators in small patches, protection of larger fragments appears to be the safest course of action for small mammal conservation. Ideally, these would be connected to smaller fragments by forested corridors containing both ground-level vegetation and canopy trees. Restoration of deficient habitat elements (e.g. coarse woody debris) may also improve the chances of retaining or restoring native mammals in urban forest fragments.

TABLE 3-1. Pearson correlations between forest structural variables in 25 forest fragments in Portland, Oregon. See Table 3-2 for codes.

	<i>DTRAIL</i>	<i>SOIL</i>	<i>HERB</i>	<i>MOSS</i>	<i>LWD</i>	<i>LITTER</i>	<i>LOW</i>	<i>MED</i>	<i>HIGH</i>
<i>DTRAIL</i>	1.000								
<i>SOIL</i>	-0.190	1.000							
<i>HERB</i>	0.165	0.246	1.000						
<i>MOSS</i>	-0.271	0.309	0.386	1.000					
<i>LWD</i>	-0.187	0.202	0.184	0.434*	1.000				
<i>LITTER</i>	0.364	-0.702*	-0.327	-0.562*	-0.162	1.000			
<i>LOW</i>	-0.204	0.295	0.031	-0.308	-0.241	-0.377	1.000		
<i>MED</i>	0.314	0.010	-0.118	0.119	0.382	0.232	-0.271	1.000	
<i>HIGH</i>	0.050	0.189	0.421*	0.631*	0.469*	-0.328	-0.319	0.307	1.000
<i>CANPY</i>	0.150	-0.223	-0.219	-0.096	0.038	0.408*	-0.531*	0.239	-0.168
<i>BASAL</i>	0.176	-0.234	-0.114	-0.282	-0.417*	0.175	0.177	-0.091	-0.421*
<i>STEMS</i>	-0.292	0.024	0.062	0.523*	0.528*	-0.083	-0.399*	-0.212	0.401*
<i>DBH30</i>	0.184	-0.088	-0.142	-0.386	-0.507*	0.165	0.106	-0.183	-0.398*
<i>CONED</i>	0.493*	-0.172	-0.142	-0.239	-0.171	0.557*	-0.395*	0.417*	-0.151
<i>ANGIOD</i>	-0.122	0.371	0.279	0.400*	0.364	-0.525*	0.068	-0.073	0.424*
<i>%CONE</i>	-0.148	-0.474*	-0.158	0.036	-0.210	0.053	0.010	-0.070	-0.218
<i>CWD</i>	0.250	-0.076	-0.105	-0.256	0.083	0.536*	-0.395*	0.406*	0.111
<i>TLOG</i>	0.439*	-0.056	0.092	0.125	0.403*	0.364	-0.567*	0.594*	0.571*
<i>TSNAG</i>	0.096	-0.137	-0.010	0.047	0.237	0.507*	-0.494*	0.216	0.005
<i>LOG20</i>	0.591	-0.064	0.112	-0.092	0.160	0.419*	-0.510*	0.516*	0.383
<i>SNAG20</i>	0.115	0.261	0.273	-0.023	-0.026	0.095	-0.170	0.178	0.153
<i>DLOG</i>	0.386	0.054	0.060	-0.166	0.206	0.442*	-0.369	0.291	0.215
<i>DSNAG</i>	0.058	-0.297	-0.025	0.054	0.216	0.597*	-0.509*	0.231	-0.037

	<i>CANPY</i>	<i>BASAL</i>	<i>STEMS</i>	<i>DBH30</i>	<i>CONED</i>	<i>ANGIOD</i>	<i>%CONE</i>	<i>CWD</i>	<i>LOG10</i>
<i>CANPY</i>	1.000								
<i>BASAL</i>	-0.220	1.000							
<i>STEMS</i>	-0.011	-0.392	1.000						
<i>DBH30</i>	-0.002	0.710	-0.446*	1.000					
<i>CONED</i>	0.391	0.230	-0.186	0.308	1.000				
<i>ANGIOD</i>	-0.107	-0.276	0.292	-0.376	-0.442*	1.000			
<i>%CONE</i>	-0.078	0.584*	-0.209	0.324	-0.027	-0.239	1.000		
<i>CWD</i>	0.333	0.013	-0.115	0.237	0.596*	-0.285	-0.225	1.000	
<i>LOG10</i>	0.204	-0.218	0.198	-0.118	0.493*	-0.120	-0.266	0.683*	1.000
<i>SNAG10</i>	0.396	-0.164	0.338	-0.007	0.547*	-0.243	-0.259	0.597*	0.568*
<i>LOG20</i>	0.322	-0.100	-0.086	0.115	0.552*	-0.253	-0.276	0.719*	0.914*
<i>SNAG20</i>	0.154	-0.077	-0.198	0.025	0.412*	-0.090	-0.437*	0.527*	0.374
<i>DLOG</i>	0.279	-0.292	0.174	0.030	0.591*	-0.205	-0.520*	0.697*	0.781*
<i>DSNAG</i>	0.296	0.019	0.381	0.008	0.451*	-0.212	-0.056	0.476*	0.468*

TABLE 3-1 (cont.):

	<i>SNAG10</i>	<i>LOG20</i>	<i>SNAG20</i>	<i>DLOG</i>	<i>DSNAG</i>
<i>SNAG10</i>	1.000				
<i>LOG20</i>	0.539*	1.000			
<i>SNAG20</i>	0.441*	0.497*	1.000		
<i>DLOG</i>	0.668*	0.775*	0.493*	1.000	
<i>DSNAG</i>	0.893*	0.394	0.175	0.461*	1.000

\* Significant at  $\alpha = 0.05$

TABLE 3-2. Pearson correlations for individual habitat variables and principal component axes among small mammal habitat elements in 25 forested sites in Portland, Oregon. For details of data collection, see Chapter 2.

Code	Habitat Variable	HAB1	HAB2	HAB3
<i>DTRAIL</i>	Mean distance to nearest trail (m)	0.464*	-0.225	0.386
<i>SOIL</i>	% cover bare mineral soil	-0.209	0.487*	0.560*
<i>HERB</i>	% cover herbaceous plants	-0.034	0.441*	0.352
<i>MOSS</i>	% cover moss	-0.120	0.732*	-0.181
<i>LWD</i>	% cover woody debris 2.5-10 cm diameter	0.194	0.705*	-0.226
<i>LITTER</i>	Mean depth organic litter layer (cm)	0.660*	-0.535*	-0.325
<i>LOW</i>	% cover of shrubs, 0.0-0.5 m	-0.637*	-0.199	0.410*
<i>MED</i>	% cover of shrubs, 0.5-1.5 m	0.536*	0.128	0.156
<i>HIGH</i>	% cover of shrubs, 1.5-3.0 m	0.192	0.769*	0.157
<i>CANPY</i>	Mean % cover, tree canopy	0.488*	-0.113	-0.265
<i>BASAL</i>	Total basal area of trees $\geq$ 2.5 cm DBH	-0.127	-0.695*	0.090
<i>STEMS</i>	Number of stems $\geq$ 2.5 cm DBH	0.085	0.620*	-0.598*
<i>DBH30</i>	Number stems $\geq$ 30 cm DBH	0.050	-0.687*	0.242
<i>CONED</i>	Simpson diversity ( $1 - \lambda$ ) of conifers	0.744*	-0.359	0.109
<i>ANGIOD</i>	Simpson diversity ( $1 - \lambda$ ) of angiosperms	-0.332	0.625*	0.094
<i>%CONE</i>	% conifers (of trees $\geq$ 2.5 cm DBH)	-0.294	-0.469*	-0.368
<i>CWD</i>	Total volume of coarse woody debris	0.817*	-0.124	0.177
<i>LOG10</i>	Number of logs $\geq$ 10 cm diameter	0.859*	0.306	0.105
<i>SNAG10</i>	Number of snags $\geq$ 10 cm DBH	0.793*	0.082	-0.283
<i>LOG20</i>	Number of logs $\geq$ 20 cm diameter	0.875*	0.070	0.295
<i>SNAG20</i>	Number of snags $\geq$ 20 cm DBH	0.506*	0.106	0.506*
<i>DLOG</i>	Number of decayed logs (class 4 or 5)	0.857*	0.156	0.185
<i>DSNAG</i>	Number of decayed snags (class 4 or 5)	0.683*	-0.012	-0.478*
	eigenvalue	6.752	4.697	2.371
	% explained	29.36	20.42	10.31

\*Significant at  $P < 0.05$ .

TABLE 3-3. Pearson correlations between geophysical and landscape variables and PCA axes for a subset of 25 forested sites in Portland, Oregon. The PCA axes were derived from a larger set of 48 sites, and are presented in Chapter 2.

Variable	GEO1	GEO2	LAND1	LAND2
Mean elevation of site	0.697*	-0.608*		
Range of elevations in site	0.861*	0.051		
Mean slope of vegetation plots	0.809*	-0.151		
Stream density (m/ha) <sup>†</sup>	0.755*	0.327		
Wetland density (m <sup>3</sup> /ha) <sup>†</sup>	-0.532*	0.837*		
% Forest			-0.756*	-0.551*
% Residential			0.932*	0.135
% Developed canopy			-0.023	-0.891*
% Treeless open space			0.345	0.854*
% Commercial-industrial			-0.280	0.366
Mean proximity of all forest patches <sup>†</sup>			-0.662*	0.134
Building density (count/ha)			0.952*	-0.011
Population density (count/ha)			0.934*	0.209
Street density (m/ha)			0.859*	-0.245

\* Significant at  $P < 0.05$ . <sup>†</sup>  $\text{Log}_{10}$  transformed.

Table 3-4: Pearson correlations between environmental axes describing local forest structure (*HAB*), geomorphology (*GEO*), landscape structure (*LAND*), patch area, and patch *SHAPE* index for 25 forest fragments in Portland, Oregon.

	<i>HAB1</i>	<i>HAB2</i>	<i>HAB3</i>	<i>GEO1</i>	<i>GEO2</i>	<i>LAND1</i>	<i>LAND2</i>	<i>AREA</i> <sup>†</sup>	<i>SHAPE</i>
<i>HAB1</i>	1.000								
<i>HAB2</i>	0.000	1.000							
<i>HAB3</i>	0.000	0.000	1.000						
<i>GEO1</i>	0.727*	-0.264	0.227	1.000					
<i>GEO2</i>	0.297	0.093	-0.187	-0.223	1.000				
<i>LAND1</i>	-0.590*	0.363	-0.054	-0.566*	-0.060	1.000			
<i>LAND2</i>	-0.030	0.200	-0.628*	-0.260	0.371	0.098	1.000		
<i>AREA</i> <sup>†</sup>	0.868*	-0.234	-0.056	0.677*	0.319	-0.671*	0.018	1.000	
<i>SHAPE</i>	0.491*	-0.352	-0.086	0.451*	0.186	-0.521*	-0.082	0.632*	1.000

\* Significant at  $P < 0.05$ . †  $\text{Log}_{10}$  transformed.

TABLE 3-5. Results of stepwise regression against species richness of small mammals in forest fragments in Portland, Oregon ( $n = 25$ ). Values represent adjusted  $R^2$  and standardized regression coefficients.

Dependent	$R^2$	$F$	$P$	Predictors	$\beta$	$P$	
Overall	0.551	15.10	0.00				
					<i>GEO2</i>	0.798	0.000
					<i>LAND</i>	-	
				2	0.495	0.003	
Native Species	0.779	27.99	0.00		0.76		
					<i>GEO2</i>	7	0.000
					<i>LAND</i>	-	
					1	0.476	0.000
				2	0.347	0.004	
Native Insectivores	0.323	10.50	0.00		0.56		
					<i>SHAPE</i>	9	0.004
Native Rodents	0.535	14.23	0.00		0.81		
					<i>GEO2</i>	1	0.000
					<i>LAND</i>	-	
				2	0.391	0.018	
Non-native Rodents	0.290	8.99	0.00		0.53		
					<i>LAND</i>	9	0.007
				1			

TABLE 3-6. Nestedness of small mammal communities from 25 forested sites in Portland, Oregon. Temperatures (*T*) and *P*-values calculated using the nestedness temperature calculator (Atmar and Paterson 1995). Statistical probabilities were calculated by Monte Carlo simulation using 50 random permutations. Idiosyncratic species have individual temperatures equal to or greater than the overall matrix temperature.

	All Mammals	Native Mammals	Native Insectivores	Native Rodents	Non-Native Rodents
Total Number of Species	14	10	3	5	4
Percent Filled	41.7	45.6	46.6	51.3	38.0
Field Data <i>T</i>	15.69	10.81	32.25	2.98	2.01
Simulation Mean <i>T</i>	58.89	52.54	32.80	47.59	40.21
S. D.	5.08	5.93	13.52	7.84	11.95
<i>P</i>	< 0.001	< 0.001	0.263	< 0.001	< 0.001
<b>Idiosyncratic Species</b>	<i>S. vagrans</i>	<i>S. vagrans</i>	-	<i>S. griseus</i>	<i>S. carolinensis</i>
	<i>Neurotrichus gibbsii</i>	<i>N. gibbsii</i>		<i>Glaucomys</i>	
	<i>Sciurus carolinensis</i>	<i>S. griseus</i>		<i>sabrinus</i>	
	<i>S. griseus</i>	<i>Tamiasciurus</i>			
	<i>S. niger</i>	<i>douglasii</i>			
	<i>Rattus norvegicus</i>	<i>Microtus oregoni</i>			
	<i>R. rattus</i>				

### Figure Legends

FIG. 3-1: Study locations in the greater Portland, Oregon metropolitan area. Small mammals were sampled in 25 second growth forest fragments in the Tualatin Mountains to the west of the Willamette River. Fragments were surrounded by a heterogeneous urban matrix consisting of residential, commercial, and open spaces, as well as canopy cover over developed areas and other forest patches (stippled).

FIG. 3-2: NMDS plot of 25 forested locations in Portland, Oregon, based on Bray-Curtis dissimilarity in small mammal communities. Stress = 0.14. Contours indicate occurrence of: (a) native rodents, (b) native insectivores and carnivores, (c) non-native rodents. Species abbreviations: SOTR, *Sorex trowbridgii*; SOVA, *S. vagrans*; NEGI, *Neurotrichus gibbsii*; MUER, *Mustela erminea*; SCCA *Sciurus carolinensis*; SCNI, *Sciurus niger*; SCGR, *S. griseus*; TADO, *Tamiasciurus douglasii*; TATO, *Tamias townsendii*; GLSA, *Glaucomys sabrinus*; PEMA, *Peromyscus maniculatus*; MIOR, *Microtus oregoni*; RANO, *Rattus norvigicus*; RARA, *R. rattus*. Environmental gradients: *HABI*, increasing forest maturity and decreasing degradation; *GEO1*, increasing topographic complexity; *GEO2*, increasing water availability and decreasing elevation; *LANDI*, decreasing forest cover and increased urbanization.

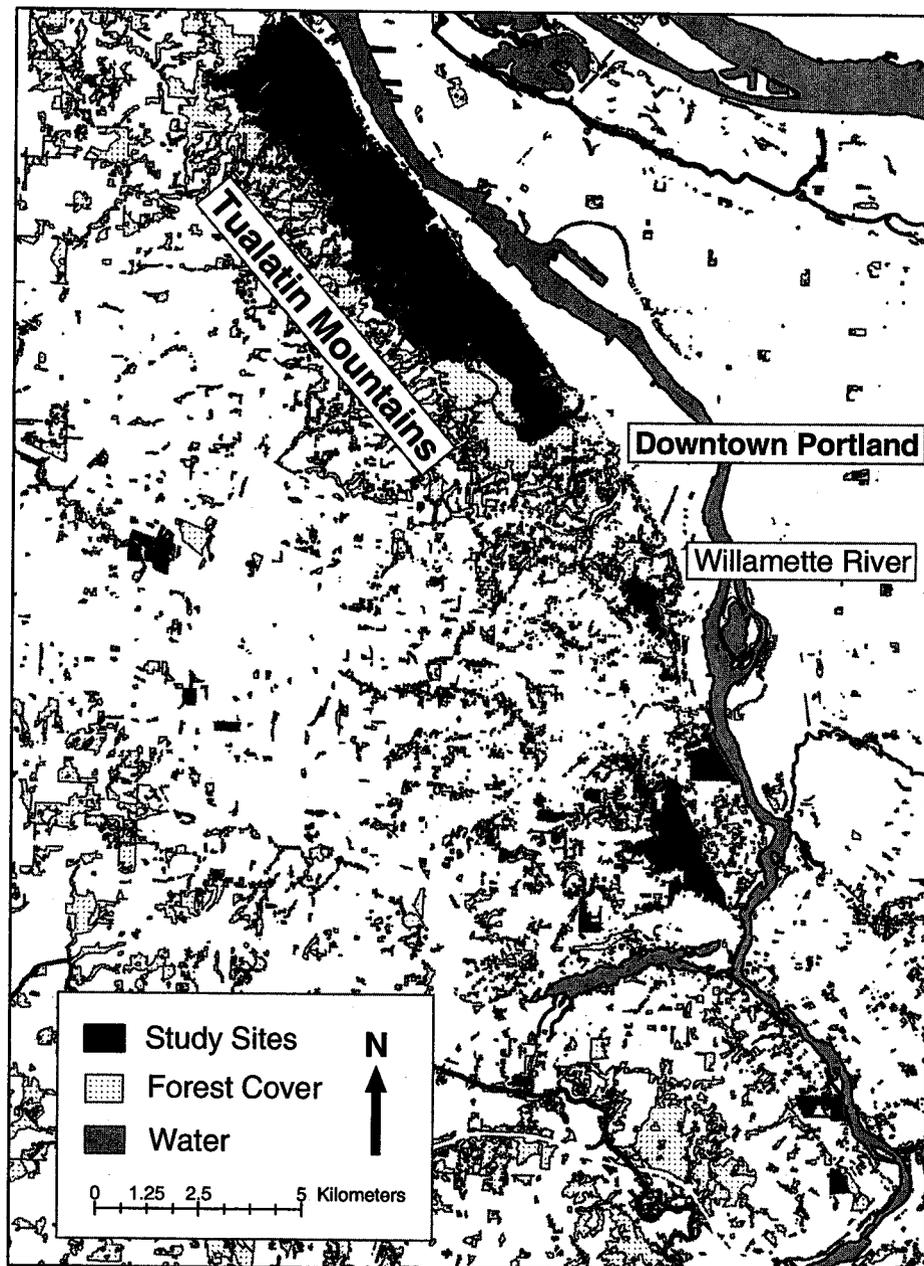


Fig. 3-1

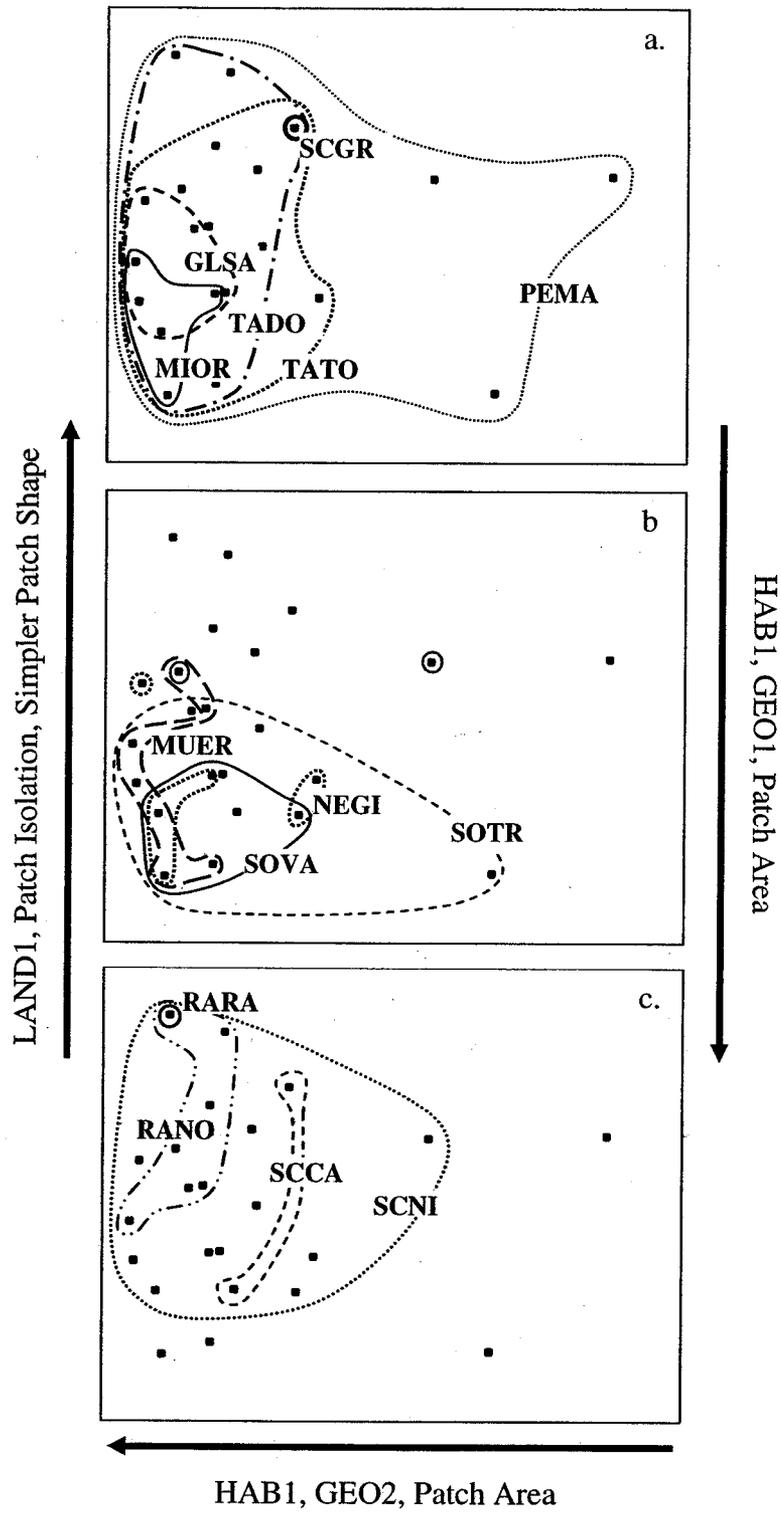


Fig. 3-2

## CHAPTER 4: CONCLUSIONS AND FUTURE DIRECTIONS

This thesis documented general biogeographic patterns in plant and small mammal communities among fragmented urban forests in Portland, Oregon. Intensification of urban development has led to the creation of many small, largely isolated forest fragments that are more subject to edge effects than are larger patches. As a result, they contain simplified plant communities and less coarse woody debris, which may have resulted in the selective local extinction of several native forest mammals, especially insectivores. Lowland sites also appear to more heavily affected than sites in the West Hills and on the eastern buttes, probably as a consequence of the challenges (both physical and governmental) of building in steeper locations. I note, however, that while the overall patterns documented here are very likely real, the mechanisms that have been proposed to underlie those patterns are hypothetical. Significant additional effort will be required to identify causal mechanisms with certainty.

Several caveats also exist with regard to the patterns themselves. In particular, the fact that certain species did not occur in our surveys does not necessarily mean that they do not occur in forest fragments in the Portland area, or even that they do not occur in the sites that we surveyed. In general, species will have been detected in proportion to their abundance, and rare or unevenly distributed species may have been,

and probably were, missed. Rarefaction curves for mammal trapping data indicate that the complete set of detected species in Tryon Creek State Park, our most diverse site, was apparent only after more than 150 animals were captured. Employment of point counts may have reduced this number, as some of the more trap-averse animals were readily detectable by direct observation (e.g. Douglas squirrels, *Tamiasciurus douglasii*). However, the mean number of animals captured per site, 80.92, was sufficiently low to warrant caution. In addition, researchers employing much heavier but more centralized trapping efforts, have continued to detect new species at Oxbow Regional Park and Forest Park over the past two years (pers. comm. L. Dizney). Some sites are known to contain animals that we missed. For example, northern flying squirrels exist in Forest Park, despite our failure to detect them there (pers. comm. L. Dizney, D. Bailey). These are, however, issues of detail that are extremely unlikely to affect the overall patterns documented in the preceding chapters. In fact, given the range in patch size among the fragments sampled and our limited surveying abilities, very small patches were proportionally sampled much more heavily than large sites. As a consequence, the differences in diversity among patches may be more intense than shown here, rather than less intense.

A more problematic (and more interesting, from a biological point of view) issue is raised by the possibility of metapopulation dynamics among our study species. We sampled forest fragments over only two years, effectively providing a single snapshot of what may very well be a dynamic, changeable landscape. If patches exhibit

extinction-recolonization dynamics, some of the absences documented in our surveys may be temporary. Longer term monitoring, possibly combined with investigations of population genetics, would be needed to detect such patterns. However, metapopulation dynamics are unlikely to affect tree communities, except over very long time spans. Consequently, the underlying patterns of habitat degradation are likely to remain, regardless of the dispersal abilities of vertebrates and smaller plants. As a result, while metapopulation function may provide some hope for community persistence and restoration, active habitat restoration will probably be required for it to have a significant impact on regional biogeography. Such restoration might include tree planting (especially of non-Douglas-fir conifers in upland sites), creation of coarse woody debris, and improvement of low shrub cover in small parks, but any methods and treatments should be tested for efficacy before being widely implemented.

This study, together with those of Bailey (unpublished) and Roberts (unpublished), was intended to lay a foundation for continued research on urban forest ecology in Portland, and does exactly that: it documents patterns and identifies hypothetical mechanisms that may have contributed to their formation. Significant experimental work will be needed to confirm or reject those hypotheses. In addition, long term monitoring of regional plant and wildlife communities is needed, both to answer questions concerning ecological processes, and to verify the success of conservation efforts under Metro's Goal 5 Initiative (Metro 2002). If sufficient

political will can be created, monitoring could also form the backbone of an experimental, adaptive management program designed not only to identify best management practices, but also to provide valuable scientific data on the effects of urban development on forests. This approach could hold particular promise if coordinated with future expansion of the urban growth boundary, effectively turning metropolitan Portland into an experimental forest. Provided sufficient resources (especially in terms of staffing and available faculty oversight), a set of senior capstone programs at Portland State University, focused on vegetation and wildlife survey techniques, might be able to supply the bulk of this monitoring effort, freeing future graduate students for more detailed experimental work.

While our research to date has made significant progress in documenting regional biogeographic patterns, many holes remain to be filled. In particular, specific information is needed concerning animal movements across the landscape and use of matrix habitats in particular. Many of the hypotheses put forward in the preceding chapters depend on such data. In addition, we have little information on population densities or demographics of Portland wildlife communities, although students in the Ruedas laboratory are producing such data for a limited number of parks. It may be possible to calibrate simpler, transect based monitoring protocols against their trapping webs to provide reliable small mammal population estimates for numerous parks with relatively little effort (this may, however, be complicated by fact that their core research requires removal sampling). Further information is also needed on carnivore

and ungulate populations in Portland-area forest fragments. Carnivores, especially free-roaming domestic cats (*Felis catus*), have great potential to affect both small mammals and birds in fragmented systems (Crooks and Soule 1999), and ungulates can have significant impacts of vegetation dynamics (Singer *et al.* 2003).

Additionally, it may be profitable to examine correlations between different land use categories and vegetation patterns. We documented consistent positive effects of canopy tree retention in the developed matrix on forest communities, a pattern also noted for birds (Hennings and Edge 2003). It would be interesting to know whether such areas differ substantially from other residential zones in their understory composition as well. Finally, as these pieces of the puzzle are filled in, it will become increasingly possible to look directly at interactions between different segments of the community, and how these interactions change with increased urbanization. Knowledge of such mechanisms will have direct and substantial implications for the conservation and management of wildlife in Portland, as well as in other urbanizing regions of the world.

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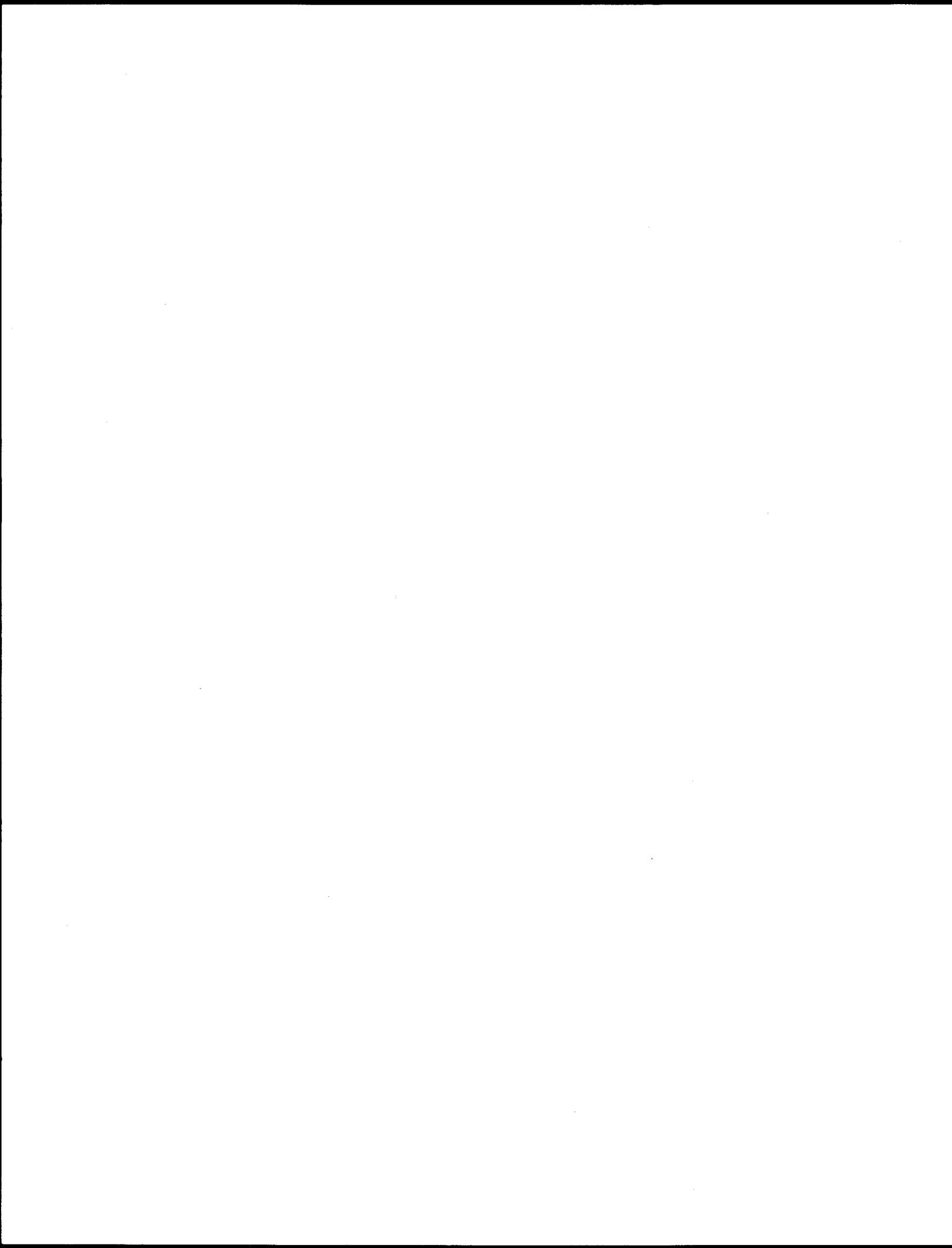
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## APPENDIX A: SITE NAMES, AREAS, AND COORDINATES

Site ID	Site Name	Area (ha)	UTM East	UTM North
1	Forest Park North	731.8	515787	5048343
2	Forest Park South	1538.4	516126	5048040
3	Columbia Park	3.6	546315	5041666
4	Nadaka Park	3.7	540442	5041795
5	Helen Athalos Park	3.7	547525	5042824
6	Marquam Park	38.9	523761	5038621
7	Tualatin Hills Nature Park	72	512255	5038387
8	Keller Woodlands	71.7	524269	5037484
9	Kane Road North	1.2	546956	5038944
10	Kelly Butte	29.3	534710	5038557
11	Kane Road South	4.4	546973	5038795
12	Oxbow Regional Park	390.1	554835	5037366
13	Powell Butte	129.0	538293	5036800
14	Gresham Butte	354.3	543765	5036395
15	Jenne Butte	49.4	540699	5036819
16	George Himes Park North	8.9	523493	5037838
17	George Himes Park South	5.7	524778	5035875
18	Fir Grove Park	1.6	514727	5035516
19	Lowami Hart Woods	11.8	513170	5034892
20	Mt. Scott Church	9.0	534842	5035407
21	Hyland Forest Park	11.7	514126	5034222
22	Woods Memorial Park	11.1	521606	5033879
23	Shaughnessie Park	0.3	513000	5033333
24	Riverview Cemetary	80.5	525858	5033645
25	Marshall Park North	10.4	524045	5033419
26	Tryon Creek State Park	288.3	525222	5031957
27	Dickinson Park	2.7	520764	5033012
28	Maricara Park	11	523088	5032862
29	Marshall Park South	22.1	524217	5033045
30	West Portland Park	14.1	522008	5032302
31	PCC Sylvania Parking Island	1.3	520970	5031962
32	Kerr Park	5.3	522209	5031769
33	Lesser Park	18.3	520827	5031511
34	Mt. Talbert	114.0	535014	5030339
35	Lake Oswego HS North	3.7	523381	5030607
36	Lake Oswego HS South	2.0	523511	5030399
37	Lake Oswego Church	0.8	524260	5030132
38	Smith Woods	7.9	524714	5030173
39	Springbrook Park	23.0	523071	5029761
40	Iron Mountain	21.8	523396	5029205
41	Walluga Park	13.8	521489	5028919
42	Durham City Park	1.4	519089	5026845

<b>Site ID</b>	<b>Site Name</b>	<b>Area (ha)</b>	<b>UTM East</b>	<b>UTM North</b>
43	Cook's Butte	17.9	523463	5026647
44	Bryant Woods Park	6.4	521728	5026173
45	Canal Acres Natural Area	13.1	521689	5025749
46	Mary S. Young State Park	47.5	528863	5025548
47	Sahallee-Illahee Park	1.8	528773	5024077
48	Wilderness Park	19.8	529367	5023597



## APPENDIX B: PLANT TAXA IDENTIFIED

Code	Scientific Name	Common Name
ABGR	<i>Abies grandis</i>	grand fir
ACCI	<i>Acer circinatum</i>	vine maple
ACMA	<i>Acer macrophyllum</i>	big leaf maple
ACMI	<i>Achillea millefolium</i>	yarrow
ACNO	<i>Acer platanoides</i>	Norway maple
ACRU	<i>Actaea ruba</i>	baneberry
ACTR	<i>Achlys triphylla</i>	vanilla-leaf
ADBI	<i>Adenocaulon bicolor</i>	pathfinder
ADPE	<i>Adiantum pedatum</i>	maidenhair fern
ALRU	<i>Alnus rubra</i>	red alder
AMAL	<i>Amelanchier alnifolia</i>	serviceberry (saskatoon)
ARME	<i>Arbutus menziesii</i>	madrone
ASCA	<i>Asarum caudatum</i>	wild ginger
ASRA	<i>Aster radulinus</i>	rough-leaved aster
ATFI	<i>Athyrium filix-femina</i>	lady fern
BEAQ	<i>Berberis aquifolium</i>	tall Oregon-grape
BENE	<i>Berberis nervosa</i>	dull Oregon-grape
BESP	<i>Betula spp.</i>	birch spp.
BRNN	<i>Brassica spp.</i>	mustard, non-native
CAOB	<i>Carex obnupta</i>	slough sedge
CIAL	<i>Circaea alpina</i>	enchanter's-nightshade
CIVU	<i>Cirsium vulgare</i>	bull thistle
CLSI	<i>Claytonia sibirica</i>	candy flower
CLSP	<i>Clematis spp.</i>	clematis spp.
COAR	<i>Convolvulus arvensis</i>	field bindweed
COCA	<i>Conyza canadensis</i>	horseweed
COCO	<i>Corylus cornuta</i>	California hazelnut
CONU	<i>Cornus nuttallii</i>	Pacific dogwood
COST	<i>Cornus stolonifera</i>	red-osier dogwood
CRDO	<i>Crataegus douglasii</i>	black hawthorne
CRSP	<i>Crataegus spp.</i>	hawthorne (non-native spp.)
CYPE	Cyperaceae spp.	sedge spp.
DACA	<i>Daucus carota</i>	Queen Anne's lace
DIFO	<i>Dicentra formosa</i>	Pacific bleeding heart
DIHO	<i>Disporum hookeri</i>	Hooke's fairybells
DISM	<i>Disporum smithii</i>	Smith's fairy bells
DREX	<i>Dryopteris expansa</i>	spiny wood fern
EPSP	<i>Epilobium spp.</i>	willow herb spp.
EQSP	<i>Equisetum spp.</i>	horsetail spp.
EUOC	<i>Euonymus occidentalis</i>	western wahoo
FRLA	<i>Fraxinus latifolia</i>	Oregon ash
FRSP	<i>Fragaria spp.</i>	strawberry spp.

<b>GASH</b>	<i>Gaultheria shallon</i>	salal
<b>GASP</b>	<i>Galium</i> spp.	beadstraw spp.
<b>GEMA</b>	<i>Geum macrophyllum</i>	large-leaved avens
<b>GERO</b>	<i>Geranium robertianum</i>	herb-robert
<b>GYDR</b>	<i>Gymnocarpium dryopteris</i>	oak fern
<b>HEHE</b>	<i>Hedera helix</i>	English ivy
<b>HODI</b>	<i>Holodiscus discolor</i>	oceanspray
<b>HYFO</b>	<i>Hypericum formosum</i>	common St. John's-wort
<b>HYTE</b>	<i>Hydrophyllum tenuipes</i>	Pacific waterleaf
<b>ILAQ</b>	<i>Ilex aquifolium</i>	English holly
<b>IMNO</b>	<i>Impatiens noli-tangere</i>	jewelweed
<b>JUNC</b>	Juncaceae spp.	rush spp.
<b>LACO</b>	<i>Lapsana communis</i>	nipplewort
<b>LAMU</b>	<i>Lactuca muralis</i>	wall lettuce
<b>LASP</b>	Labiatae spp.	mint spp. (non-native)
<b>LISP</b>	Liliaceae spp.	lilly spp.
<b>LOCI</b>	<i>Lonicera ciliosa</i>	orange honeysuckle
<b>LOIN</b>	<i>Lonicera involucrata</i>	black twinberry
<b>LUAN</b>	<i>Lunaria annua</i>	honesty
<b>MADI</b>	<i>Maianthemum dilatatum</i>	false lilly-of-the-valley
<b>MAFU</b>	<i>Malus fusca</i>	Pacific crab apple
<b>MAOR</b>	<i>Marah</i> spp.	wild cucumber
<b>MASP</b>	<i>Malus</i> spp.	apple spp. (non-native)
<b>MOUN</b>	<i>Monotropa uniflora</i>	Indian-pipe
<b>NEPA</b>	<i>Nemophila parviflora</i>	small flowered nemophila
<b>OECE</b>	<i>Oemleria cerasiformis</i>	Indian-plum
<b>OESA</b>	<i>Oenanthe sarmentosa</i>	Pacific water-parsley
<b>OSCH</b>	<i>Osmorhiza chilensis</i>	mountain sweet-cicely
<b>OXOR</b>	<i>Oxalis oregona</i>	redwood sorrel
<b>PHCA</b>	<i>Physocarpus capitatus</i>	Pacific ninebark
<b>PHHA</b>	<i>Phacelia hastata</i>	silverleaf phacelia
<b>PHLE</b>	<i>Philadelphus lewisii</i>	mock-orange
<b>PINK</b>	Caryophyllaceae spp.	pink family
<b>PIPO</b>	<i>Pinus ponderosa</i>	ponderosa pine
<b>PLSP</b>	<i>Plantago</i> spp.	Plantain spp.
<b>POAC</b>	Poaceae spp.	grass spp.
<b>POBA</b>	<i>Populus balsamifera</i>	black cottonwood
<b>POGL</b>	<i>Polypodium glycyrrhiza</i>	licorice fern
<b>POMU</b>	<i>Polystichum munitum</i>	sword fern
<b>POSP</b>	<i>Populus</i> spp.	poplar spp.
<b>PRCE</b>	<i>Prunus cerasus</i>	sour cherry
<b>PREM</b>	<i>Prunus emarginata</i>	bitter cherry
<b>PRLA</b>	<i>Prunus laurocerasus</i>	English laurel
<b>PRVU</b>	<i>Prunella vulgaris</i>	self-heal
<b>PSME</b>	<i>Pseudotsuga menziesii</i>	Douglas fir
<b>PTAQ</b>	<i>Pteridium aquilinum</i>	bracken fern

QUGA	<i>Quercus garryana</i>	Oregon white oak
RARE	<i>Ranunculus repens</i>	creeping buttercup
RHPU	<i>Rhamnus purshiana</i>	cascara
RONN	<i>Rosa</i> spp.	rose spp. (non-native)
ROSP	<i>Rosa</i> spp.	rose spp. (native)
STRO	<i>Streptopus roseus</i>	Rosy twisted-stalk
RUDI	<i>Rubus discolor</i>	Himalayan blackberry
RULE	<i>Rubus leucodermis</i>	blackcap raspberry
RUME	<i>Rumex</i> spp.	dock spp.
RUOC	<i>Rumex occidentalis</i>	western dock
RUPA	<i>Rubus parviflorus</i>	thimbleberry
RUSP	<i>Rubus spectabilis</i>	salmonberry
RUUR	<i>Rubus ursinus</i>	trailing blackberry
SADO	<i>Satureja douglasii</i>	yerba buena
SARA	<i>Sambucus racemosa</i>	red elderberry
SASP	<i>Salix</i> spp.	willow spp.
SMRA	<i>Smilacina racemosa</i>	false solomon's seal
SMST	<i>Smilacina stellata</i>	star-flowered false Solomon's seal
SODU	<i>Solanum dulcamara</i>	European bitter-sweet
SOSP	<i>Sorbus</i> spp.	mountain ash spp.
SPDO	<i>Spiraea douglasii</i>	Douglas spiraea
STCO	<i>Stachys cooleyae</i>	Cooley's hedge-nettle
STCR	<i>Stellaria crispa</i>	crisp sandwort
STME	<i>Stachys mexicana</i>	Mexican hedge-nettle
SYAL	<i>Symphoricarpos albus</i>	common snowberry
TABR	<i>Taxus brevifolia</i>	western yew
TAOF	<i>Taraxacum officinale</i>	common dandelion
TEGR	<i>Tellima grandiflora</i>	fringecup
THPL	<i>Thuja plicata</i>	western red cedar
TITR	<i>Tiarella triflata</i>	foamflower
TODI	<i>Toxicodendron diversilobum</i>	poison oak
TOME	<i>Tolmiea menziesii</i>	piggy-back plant
TRCA	<i>Trautvetteria caroliniensis</i>	false bugbane
TRLA	<i>Trientalis latifolia</i>	western starflower
TROV	<i>Trillium ovatum</i>	western trillium
TRSP	<i>Trifolium</i> spp.	clover, non-native
TSHE	<i>Tsuga heterophylla</i>	western hemlock
URDI	<i>Urtica dioica</i>	stinging nettle
VAHE	<i>Vancouveria hexandra</i>	inside-out flower
VAPA	<i>Vaccinium parvifolium</i>	red huckleberry
VERI	<i>Veratrum californicum</i>	California false hellebore
VIGL	<i>Viola glabella</i>	yellow wood violet
VIMI	<i>Vinca minor</i>	periwinkle
WISE	<i>Viola sempervirens</i>	evergreen violet
VISP	<i>Vicia</i> spp.	vetch spp.
XAST	<i>Xanthium strumarium</i>	common cocklebur

## APPENDIX C: SITE SPECIES LISTS

Site	ABGR	ACCI	ACMA	ACMI	ACNO	ACRU	ACTR	ADBI	ADPE	ALRU	AMAL	ARME
1	X	X	X			X	X		X	X		
2	X	X	X				X		X	X		
3		X	X									
4		X	X									X
5		X	X							X		
6		X	X						X	X	X	
7	X	X					X	X		X	X	
8	X	X	X				X		X	X		
9			X									
10		X	X				X					X
11			X									
12		X	X						X			
13		X	X							X	X	
14		X	X							X		
15		X	X							X		
16		X	X	X						X		
17		X	X							X		
18		X	X					X				
19		X									X	X
20			X			X	X					
21		X	X								X	
22		X	X							X		
23												
24	X	X	X							X		
25	X	X	X				X			X		
26	X	X	X				X			X		
27		X	X							X		
28		X	X				X			X		
29	X	X	X				X		X	X		
30		X	X							X		
31			X							X		
32		X	X							X		
33	X	X	X				X	X		X	X	
34		X	X							X	X	
35			X		X							
36		X	X								X	
37		X	X							X		
38		X	X							X		
39			X							X	X	
40		X	X								X	
41		X	X							X	X	X
42			X							X		

43		X	X					X		X	X
44		X	X							X	
45		X	X							X	X
46	X	X	X							X	
47		X	X								
48		X	X					X			

Site	ASCA	ASRA	ATFI	BEAQ	BENE	BESP	BRNN	CAOB	CIAL	CIVU	CLSI	CLSP
1	X		X		X						X	
2	X		X		X						X	
3									X		X	
4									X		X	
5												
6			X		X						X	X
7	X		X		X			X	X		X	
8	X		X		X						X	X
9				X								
10					X							
11					X		X					
12			X						X		X	
13	X				X				X		X	
14					X						X	
15					X				X		X	
16			X	X	X				X			X
17			X		X							
18					X							X
19		X		X	X	X		X				
20					X				X		X	X
21			X		X							X
22			X		X				X			
23				X			X			X		
24			X		X						X	X
25					X							
26	X		X		X				X		X	X
27			X		X				X			X
28					X				X		X	
29			X		X							
30	X		X		X						X	
31					X							X
32					X				X		X	X
33					X	X			X	X	X	
34					X		X		X		X	
35					X							X
36					X							

37												
38			X		X							
39					X				X			
40		X			X							X
41												X
42					X							
43	X				X					X		
44								X	X			
45					X			X	X			
46			X						X			
47			X		X						X	
48					X							

Site	COAR	COCA	COCO	CONU	COST	CRDO	CRSP	CYPE	DACA	DIFO	DIHO	DISM
1			X								X	
2			X								X	X
3			X							X		
4			X									
5			X									
6			X	X							X	
7			X	X	X	X	X	X			X	
8			X	X							X	
9				X				X				
10			X	X			X				X	
11		X	X					X				
12			X					X			X	
13			X	X	X		X	X			X	
14			X				X	X		X	X	
15			X					X		X	X	
16			X					X			X	
17			X								X	
18			X	X								
19			X	X	X		X	X				
20			X	X							X	
21			X				X					
22	X		X	X								
23							X					
24			X		X			X			X	
25			X								X	
26			X					X				
27			X			X	X	X		X	X	
28			X					X			X	
29			X					X			X	
30			X					X			X	

31		X						X				
32		X						X				
33		X	X					X	X			X
34		X					X	X				X
35		X										
36		X	X					X				
37		X						X				
38		X										
39		X			X	X		X				X
40		X	X					X	X	X		
41		X						X				
42		X										
43		X	X				X	X	X			X
44		X						X	X			
45		X	X	X				X	X			
46		X	X									
47		X										
48		X	X						X			X

Site	DREX	EPSP	EQSP	EUOC	FRLA	FRSP	GASH	GASP	GEMA	GERO	GYDR	HEHE
1							X	X		X	X	
2							X	X		X		
3								X				X
4							X	X		X		
5								X				X
6					X		X	X	X	X		X
7					X	X	X	X				
8						X	X	X	X	X		X
9								X		X		
10					X			X				X
11								X		X		
12	X							X				
13								X				
14		X						X	X			
15								X				
16			X					X	X	X		X
17								X	X			X
18								X				X
19				X	X		X	X	X			X
20								X				X
21					X		X			X		X
22							X					X
23								X				
24			X		X		X	X				X

25			X				X					X
26		X	X				X	X		X		X
27		X			X			X	X	X		X
28							X	X	X	X		X
29		X	X					X	X	X		X
30									X			X
31							X	X	X	X		
32							X	X	X			
33					X		X	X	X	X		X
34					X		X	X				
35							X	X				X
36							X					X
37										X		X
38		X						X	X			X
39			X		X		X	X	X	X		X
40			X		X		X	X		X		X
41							X					X
42										X		X
43				X			X	X		X		X
44		X		X			X		X			X
45		X		X			X	X	X	X		X
46			X	X								X
47								X		X		X
48							X	X	X			X

Site	HODI	HYFO	HYTE	ILAQ	IMNO	JUNC	LACO	LAMU	LASP	LISP	LOCI	LOIN
1	X		X							X		
2			X	X						X		
3			X					X				
4							X	X				
5			X				X					
6	X		X	X			X					
7	X		X	X				X		X		
8	X		X	X						X	X	
9							X	X				
10	X			X							X	
11			X	X			X					
12			X					X				
13	X		X	X			X	X		X		
14	X	X	X	X	X		X	X				
15			X	X	X					X	X	
16	X		X	X			X			X		
17			X	X								
18				X			X	X				

19	X			X			X			X	X
20			X	X							
21	X			X							
22			X	X							
23				X			X				
24			X	X					X	X	
25			X	X							
26			X	X	X						
27			X								
28	X		X	X				X		X	
29			X	X		X					
30			X	X							
31			X				X				
32	X		X								
33	X		X	X							
34	X		X	X					X		
35			X	X							
36				X							
37			X	X					X		
38			X	X							
39	X		X	X				X			
40	X	X					X				
41	X										
42											X
43	X		X	X			X	X			
44	X		X								
45			X	X		X					X
46			X	X							
47			X				X				
48	X		X	X							

Site	LUAN	MADI	MAFU	MAOR	MASP	MOUN	NEPA	OECE	OESA	OSCH	OXOR	PHCA
1		X						X				
2		X						X		X		
3							X	X				
4												
5											X	
6								X		X		
7			X				X	X				X
8							X	X		X		
9												
10							X					
11								X				
12				X			X	X		X	X	

13							X	X		X		
14							X	X		X		
15							X	X		X		
16								X				
17								X	X			
18												
19								X				
20								X		X		
21												
22								X				
23				X								
24								X				
25								X				
26				X				X	X			
27		X							X			X
28								X				
29								X	X			
30						X		X				
31											X	
32								X				
33							X				X	
34		X					X				X	
35												
36								X				
37		X		X				X				
38								X				
39		X						X				
40	X						X					
41		X										X
42												
43				X						X		X
44								X				
45								X				X
46								X				X
47								X				
48								X				

Site	PHHA	PHLE	PINK	PIPO	PLSP	POAC	POBA	POGL	POMU	POSP	PRCE	PREM
1			X			X			X			
2						X			X			
3						X			X		X	
4						X			X		X	
5												
6						X		X	X		X	

7		X	X		X	X		X		
8		X			X		X	X		X
9					X			X		X
10		X			X		X	X		X
11				X	X				X	
12		X	X		X		X	X		X
13					X			X		X
14	X		X		X		X	X		
15			X		X		X	X		X
16					X			X		
17								X		X
18					X			X		X
19		X		X	X			X		X
20								X		X
21					X			X		X
22					X			X		X
23					X					
24			X		X	X		X		X
25					X		X	X		X
26					X	X	X	X	X	
27					X			X		X
28					X			X		X
29					X		X	X		X
30					X		X	X		
31					X			X	X	
32					X			X		X
33					X	X	X	X		X
34			X		X		X	X		X
35								X		X
36								X		X
37								X		
38								X		
39					X	X	X	X		X
40				X	X		X	X		X
41		X				X	X	X		X
42								X		X
43		X			X	X	X	X		X
44							X	X		
45					X			X		
46						X	X	X		
47		X						X		
48								X		X



45		X	X		X		X	X		X
46		X			X					X
47		X								X
48		X	X				X			X

Site	RUME	RUOC	RUPA	RUSP	RUUR	SADO	SARA	SASP	SMRA	SMST	SODU	SOSP
1				X	X		X		X			
2			X	X	X		X		X			
3			X		X						X	
4					X						X	
5				X								
6			X	X	X		X		X			
7			X		X	X	X	X		X	X	
8			X		X		X		X	X		X
9					X							
10			X		X				X	X		
11					X						X	X
12				X	X		X					
13					X		X					
14	X		X	X	X		X				X	X
15				X	X		X			X		
16		X	X		X		X					
17			X		X		X		X			
18					X							
19		X	X		X			X				
20			X		X		X		X	X		
21			X		X		X				X	
22			X		X		X					X
23					X							
24	X		X		X							X
25				X	X							
26			X	X	X		X					
27					X		X	X			X	
28			X		X		X		X			
29			X	X	X		X		X			
30			X	X	X		X					X
31			X		X		X	X		X		
32			X		X		X	X				
33			X		X				X	X		X
34			X		X							
35			X		X		X					
36					X			X				X
37					X		X					
38			X	X	X							

39		X		X		X	X					X
40		X		X		X						
41					X	X			X			
42					X			X				
43			X		X			X	X			
44			X		X							
45	X		X		X				X			
46				X	X			X				
47			X	X	X							
48			X	X	X			X				

Site	SPDO	STCO	STCR	STME	SYAL	TABR	TAOF	TEGR	THPL	TITR	TODI	TOME
1			X		X	X		X	X			X
2								X	X	X		X
3				X	X			X				
4					X		X					
5					X			X	X			X
6						X		X	X			X
7					X	X			X	X	X	X
8		X			X			X	X		X	X
9					X			X	X			
10					X	X		X				
11					X			X				
12					X			X	X	X		X
13				X	X			X	X	X		X
14		X			X			X		X		X
15					X			X	X			X
16					X			X	X			X
17		X						X	X			X
18					X							
19					X		X	X	X		X	X
20								X				
21					X							
22								X	X			X
23					X			X			X	
24		X			X	X			X			
25								X	X			
26					X			X	X			X
27	X	X			X			X				
28					X			X				
29								X	X			X
30		X	X		X			X	X	X		X
31								X				
32								X				X

33					X			X		X		
34				X	X			X	X		X	X
35												
36												
37												
38								X	X			X
39					X	X		X	X			
40											X	
41					X						X	
42					X							
43					X			X			X	
44					X			X				
45	X				X			X				X
46					X	X		X				
47				X	X				X			
48					X							

Site	TRCA	TRLA	TROV	TRSP	TSHE	URDI	VAHE	VAPA	VERI	VIGL	VIMI	WISE
1		X			X		X	X		X		
2		X			X	X	X	X		X		X
3			X							X		
4								X				
5			X									
6		X			X		X	X		X		
7		X	X			X	X	X				
8		X			X		X	X		X		
9												
10		X				X	X					
11											X	
12		X	X		X			X				
13			X				X	X		X		
14			X					X				
15			X					X				
16		X					X			X		
17		X			X		X					
18							X					
19							X					
20	X		X				X	X				
21		X					X					
22							X	X				
23												
24		X			X		X	X		X		
25		X			X		X					
26		X	X		X	X	X	X				

27						X		X	
28	X					X	X		X
29	X			X		X			
30	X					X	X		X
31	X				X	X			
32						X	X		
33	X			X		X	X		X
34	X	X			X	X			X
35						X			
36									
37			X						
38			X						
39	X	X		X	X	X	X		
40				X					
41						X			
42							X		
43	X	X			X	X			X
44				X		X			
45	X	X				X			
46	X	X					X		
47	X					X			
48	X	X		X		X			X

Site	VISP	XAST
1	X	
2		
3		
4		
5		
6	X	
7		
8		
9		
10		
11		X
12		
13	X	
14	X	
15		
16		
17		
18		
19		
20		

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21	
22	
23	X
24	X
25	

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26	
27	
28	
29	
30	

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31	
32	
33	
34	X
35	

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36	
37	
38	
39	
40	X

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41	X
42	
43	
44	
45	

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46	
47	
48	

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## APPENDIX D: RELATIVE ABUNDANCES OF SMALL MAMMALS

Transects	SOTR	SOVA	NEGI	TATO	SCCA	SCGR	SCNI	TADO	GLSA	PEMA	MIOR	RANO	RARA	MUER
Canal Acres Natural Area	2	0	0	9	0	0	2	7	0	28	0	0	0	0
Dickinson Park	1	0	0	0	0	0	1	3	0	6	0	1	0	0
Forest Park North	8	3	3	8	0	0	0	4	0	58	0	0	0	1
Forest Park South	8	8	3	2	14	0	0	5	0	67	5	0	0	1
George Himes Park South	2	1	0	1	0	0	1	3	0	44	0	5	0	1
Hyland Forest Park	4	0	0	0	0	0	1	4	0	22	0	4	2	0
Keller Woodlands	6	1	0	13	0	0	4	5	2	49	1	3	0	1
Kerr Park	2	0	0	5	0	0	2	2	0	41	0	2	0	0
Lake Oswego Church	1	0	0	1	0	0	1	1	0	9	0	0	0	0
Lake Oswego HS North	1	0	1	0	0	0	2	0	0	11	0	0	0	0
Lesser Park	4	2	2	1	1	0	0	6	0	61	0	0	0	0
Lowami Hart Woods	4	0	0	10	1	4	5	7	0	52	0	0	0	0
Marcara Park	4	0	0	0	0	0	3	2	0	43	0	1	0	0
Marshall Park North	4	1	2	0	28	0	2	3	0	33	0	1	0	0
Marshall Park South	4	1	1	0	10	0	3	2	1	32	0	4	0	1
Mary S. Young State Park	2	2	0	2	0	0	2	5	1	33	0	1	0	0
PCC Sylvania Parking Island	1	0	1	0	0	0	0	0	0	19	0	0	0	0
Riverview Cemetary	8	2	0	36	0	0	3	1	7	128	2	0	0	3
Shaughnessie Park	1	0	0	0	0	0	0	0	0	3	0	0	0	0
Smith Woods	1	2	1	4	1	0	1	3	1	21	0	0	0	0
Springbrook Park	2	1	0	2	0	0	3	3	0	43	0	0	0	0
Tryon Creek State Park	10	18	4	0	17	0	1	4	1	136	11	0	0	2
Tualatin Hills Nature Park	6	2	1	0	13	1	0	7	0	41	1	0	0	0
West Portland Park	4	2	0	1	2	0	2	4	0	43	0	0	0	0
Wilderness Park	2	0	0	1	3	0	1	2	1	30	0	0	0	0

Note: abundance based on maximum estimate of minimum number known alive from 2002-2003 trapping and point counts