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Effects of Habitat and Landscape Structure on Oregon White Oak (*Quercus garryana*) Regeneration Across an Urban Gradient

Abstract

Oregon white oak (*Quercus garryana*) woodlands are the focus of intensive conservation efforts. However, little is known about regeneration in protected oak stands, particularly in small stands surrounded by residential and commercial development. This study investigates the relationship between habitat and landscape structure and patterns of oak seedling and sapling abundance. Specifically, I ask whether patterns of oak seedling and sapling abundance reflect the habitat preferences of animals that disperse acorns and whether seedling and sapling abundance differ in urban versus non-urban landscapes. I conducted vegetation surveys within 30 oak woodlands with natural understory distributed across a gradient of urban development. I used general linear mixed models to determine relationships between oak seedling and sapling abundance and habitat and landscape features. Seedling and sapling patterns showed different relationships to habitat and landscape structure, suggesting that different factors mediate the transition between each stage. I found that seedlings are most abundant under oak and non-oak forest canopy and least abundant under no forest canopy, possibly reflecting dispersal patterns. I found no relationship between seedling abundance and urban development, but young saplings show a negative relationship with urban development. These results suggest that seed dispersers influence seedling spatial patterns, but that this influence is reduced in later life history stages. Although urban development is not related to seedling production, young sapling abundance was significantly lower in urban landscapes. Improved understanding of how habitat and landscape structure influence forest regeneration processes is needed in order to create effective forest restoration and management plans.

Introduction

In recent decades, expansion of residential and commercial development has replaced much of the existing forest cover in the Puget Sound region (Alig and White 2007). These land-cover changes have lead to a significant decline in the quantity and quality of Oregon white oak (*Quercus garryana* Douglas ex Hook.) habitat. Oregon white oak is the only native oak species in Washington State and therefore represents a unique element of the region's biodiversity. In addition, oak habitats support a rich diversity of flora and fauna and are ecologically important as acorns provide a critical food resource for a wide range of wildlife, including the state-threatened Western gray squirrel (*Sciurus griseus*) (Larsen and Morgan 1998). Finally, oak systems are culturally valued throughout the world (Hougner et al. 2006, Fisher and Bliss 2008, Acacio et al. 2010). As a result, Oregon white oaks are the subject of significant restoration and protection efforts throughout their range (Larsen and Morgan 1998, Fuchs 2001, MacDougall et al. 2004). In Pierce and Thurston counties, Washington, oak stands are designated as critical areas and

therefore receive special protection during the development process (Pierce County, Ord. 2004-56s § 4 (part), 2004, Thurston County, Ord. 12463 §§ 2, 3, 200). Oak protection efforts have resulted in numerous oak stands embedded in a developed landscape. However, little is known about whether these protected urban stands are able to regenerate.

Urban areas present significantly altered environmental conditions that potentially affect oak regeneration. First, urban development alters the diversity, abundance and possibly behavior of species available to disperse acorns. Research has shown that adding or removing dispersal species at a particular location can alter seed dispersal patterns, leading to shifts in plant species composition as some seeds are no longer dispersed or may be dispersed to different locations (Christian 2001). In addition, seed dispersal often increases germination and survival and so the loss of animal dispersers can lead to higher seed predation and lower germination success (Asquith et al. 1999, Moore and Swihart 2007). Oregon white oaks are dependent upon animal dispersers including Steller's jays (*Cyanocitta stelleri*), western gray squirrels (*Sciurus griseus*), and eastern gray squirrels (*Sciurus carolinensis*). These animals provide two important services that both increase germination and survival: they carry acorns away from the parent tree,

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reducing density dependent mortality (Janzen 1970, Howe and Miriti 2000); and they bury or cache acorns, reducing the risk of desiccation (Fuchs et al. 2000a). In the study region, western gray squirrels are not known to occupy forest patches in urban areas (Ryan and Carey 1995), whereas eastern gray squirrels are abundant in urban landscapes. In addition, Steller's jays are more abundant in suburban than in urban or wildland areas (Vigallon and Marzluff 2005).

In addition to altering the presence and absence of a species, urban areas often have a higher abundance of fewer species (Blair 1996, Shochat et al. 2004), which may result in altered ecological processes. In the case of Oregon white oak, animal dispersers are also seed predators. Browers and Breland (1996) found higher rates of seed removal from experimental food stations near houses and buildings compared to stations in rural areas, which they suggest may be due to a higher density of squirrels in developed areas. The lack of large predators in urban areas can also lead to altered trophic dynamics (Shochat et al. 2004), possibly leading to a higher abundance of seed predators and seedling herbivores.

Several studies have demonstrated that spatial patterns at the site and landscape scales influence seed dispersal and subsequent seedling recruitment patterns (Garcia and Obesco 2003, McEuen and Curran 2004, Herrera and Garcia 2010). For animal-dispersed seeds, the behavior and habitat preferences of animal dispersers interact with the spatial structure of the landscape to produce the observed patterns of seed deposition (Russo et al. 2006). If animal dispersers prefer particular habitat types, these behavioral preferences may be reflected in patterns of seedling abundance. For the Oregon white oak, research has shown that their animal dispersers appear to have specific habitat preferences. For example, Fuchs and others (2000b) found that Steller's jays prefer to cache acorns in areas with abundant tree and shrub cover, but sparse herb cover. In addition, telemetry data collected for eastern and western gray squirrels show that these squirrels prefer to remain under forest canopy. Preferences for specific understory types are less clear. Western gray squirrels often occupy areas with open, sparse understory, while eastern gray squirrels occupy areas with abundant shrub cover (Aaron Johnston, University of Washington, personal communication).

In this study, I ask two questions: 1) do patterns of oak seedling and sapling abundance differ depending on canopy and understory conditions; and 2) do patterns of seedling and sapling abundance differ in urban versus non-urban landscapes? First, I hypothesize that seedling abundance will be higher in habitat types preferred by jays and squirrels. Specifically, I expect *seedling* abundance will be higher under forest canopy because it is a preferred habitat for squirrels and preferred caching habitat for jays. Disperser preferences for understory type differ by species; thus, both shrub and open understory habitats may have greater seedling abundance than grass-dominated understory habitats. Alternatively, rodent seed predation is often higher under shrub cover (Fuchs et al. 2000b, Kollmann and Buschor 2002, Perez-Ramos and Marañón 2008), suggesting that seedling emergence may be lower in this understory type. Finally, western gray squirrels have an extremely restricted range in western Washington, suggesting that fewer acorns may be dispersed to open understory habitats. Consequently, my second hypothesis is that *seedling* abundance will not have a strong relationship to understory conditions. Third, I hypothesize that *sapling* abundance will have a weaker relationship with disperser habitat preferences than seedlings. This is because the factors mediating the transition from seedling to sapling (e.g., herbivory), are likely to differ from those that influence the acorn to seedling stage. Lastly, I expect that both *seedling and sapling* abundance will be lower in oak woodlands surrounded by urban development. Areas with moderate to high densities of residential and commercial development often support a higher density of acorn predators, including eastern gray squirrels and Steller's jays, and herbivores such as deer and rabbits, which could suppress seedling emergence and survival in these areas.

Study Area

This study was conducted in the southern end of the Puget Sound Trough within the western third of Pierce and Thurston Counties, WA (Figure 1). Oregon white oaks often form relatively distinct stands (referred to here as oak woodlands), which are distributed throughout the region from the highly urbanized Tacoma metropolitan region in the north, through Joint Base Lewis-McChord (JBLM) Military installation and into rural sections of Pierce and Thurston Counties to the south. Mean annual precipitation is approximately 96 cm annually in Tacoma, but averages only four cm per month during the growing season between April and September (WRCC 2010). JBLM is over 35,000 ha and contains both extensive areas of relatively undeveloped land and significant housing, commercial, and office development. As a result, this region provides a unique opportunity to study the effects of residential and commercial development on Oregon white oak stand structure and regeneration processes.
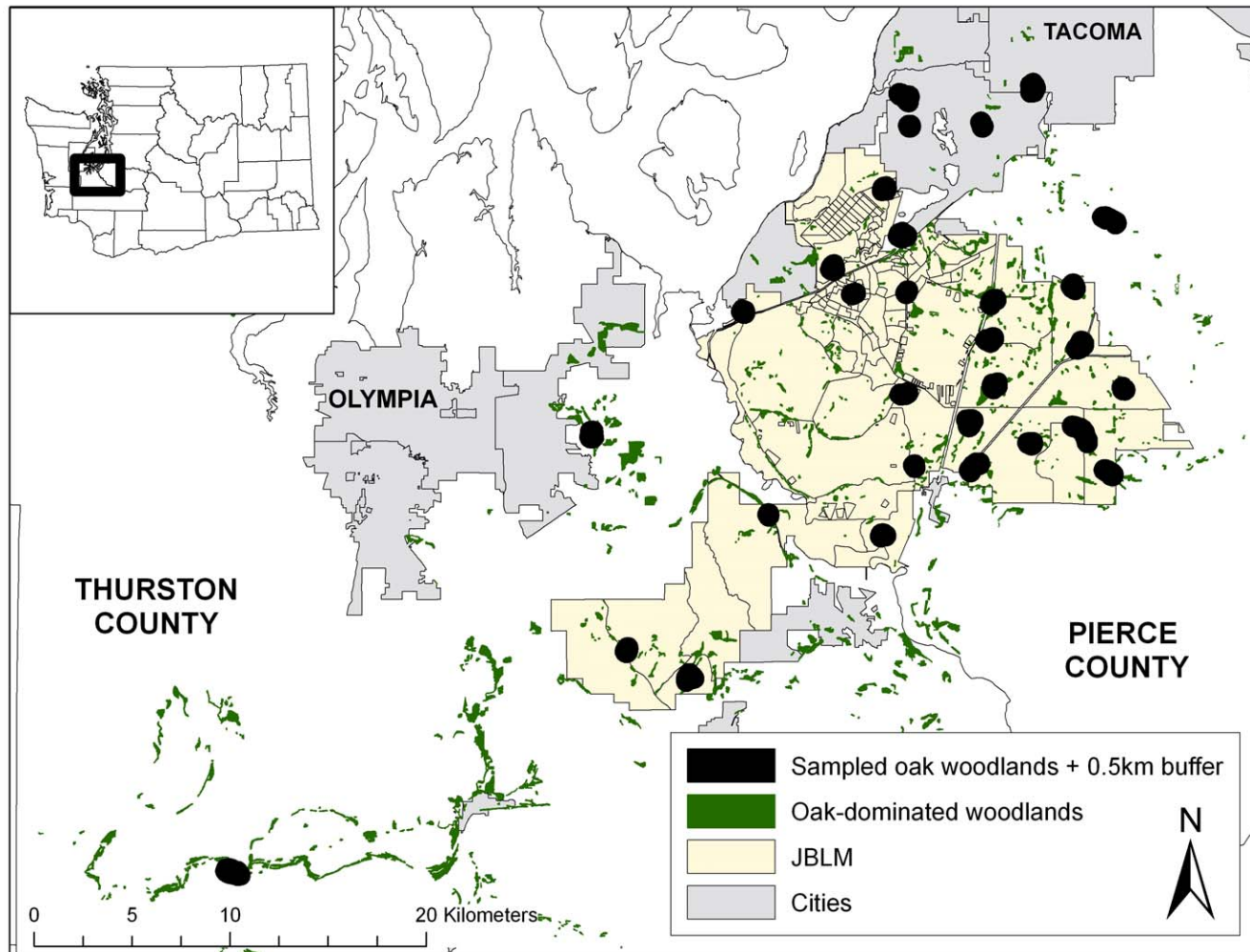
Figure 1. Distribution of Oregon white oak in western Washington. Study area indicated by box.

Methods

Site Selection

I randomly selected 45 sites from a subset of oak-dominated woodlands from a GIS database created by the Washington Natural Heritage Program. The Heritage Program defines oak-dominated stands as having greater than 25% crown canopy cover of Oregon white oak in the upper canopy layers and less than 25% crown cover of conifers with a minimum stand size threshold of approximately one acre. To reduce variation in within-stand characteristics, the subset consisted of woodlands between one and 10 ha. The stand size range was chosen to capture the majority of oak woodlands in the database while minimizing variation in woodland size. Of all the oak-dominated woodlands in the study area, 90% were smaller than 10 ha. Oak woodlands less than one ha were also excluded to avoid including woodlands with only a few oak trees.

Ultimately, 62% of all the oak-dominated woodlands in the study area fell within the size range selected. All sites were located on public lands and sites were discarded from the sample if site visits revealed that they were not accessible or had understory dominated by manicured lawns or pavement. As a result, all sites had understory vegetation that would permit natural forest regeneration. A total of 30 sites met my criteria and were included in the study. Elevation of the study area ranges from 10 to 200 m a.s.l. and all woodlands were located on gravelly or fine sandy loam soils in the Everett-Spanaway-Nisqually complex (Pierce County soils data, JBLM soils data, and Thurston County soils data).

Landscape Measurement Methods

I defined a "landscape" as the area within a 0.5 km of each oak woodland site. I chose this distance because field research has indicated that it captures the approxi-

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mate perceptual range of gray (*Sciurus carolinensis*) and fox (*Sciurus niger*) squirrels (Zollner 2000). Landscape areas did not overlap for any of the selected oak woodlands. I calculated the percent urban cover for each oak woodland landscape using ArcGIS 9.3 and a 30-m land-cover data layer derived from Landsat TM and ETM data for the Puget Sound region (Alberti et al. 2006). Urban cells were defined as those with > 50% impervious surface. Urban development was related to oak measures as both a continuous and categorical variable. The categorical variable classified each oak woodland as either urban (> 40% urban cover within 0.5 km) or non-urban (< 40% urban cover). The 40% threshold was chosen because none of the woodlands surveyed had between 25-40% urban cover creating a clear break between urban and non-urban sites. I calculated the area of each woodland in ArcGIS based on the boundaries delineated by the Heritage Program. I also used a dummy variable to indicate whether the woodland was located on or off JBLM.

Vegetation Survey Methods

I collected oak stand vegetation data within 10-m radius plots nested within each of the 30 oak woodland sites. Plot center locations were randomly generated using Hawths Tools in ArcGIS 9.3 and located in the field using a Garmin GPS. Each site had two to ten plots, depending on the woodland size. Within each plot, I collected diameter at breast height (DBH) for all oak trees with a DBH greater than 2.5 cm. DBH was measured for all other trees larger than 10 cm DBH. All oak saplings were counted and binned into two size classes. Class 1 (young) saplings were <2.5 cm DBH and 0.5-2 m tall. Class 2 (old) saplings were > 2 m tall and < 10 cm DBH. I counted oak seedlings (< 0.5 m tall) in four 1-m radius subplots. The center of each subplot was located 5 m in each cardinal direction (N, S, E, and W) of the 10-m radius plot center.

Canopy and understory composition were visually estimated for the 10-m plot and each of the 1-m seedling subplots. Both canopy and understory were analyzed separately as continuous (Table 1) and categorical variables. To create canopy categories, I binned the 1-m subplots into one of three canopy composition categories: 1) some oak canopy present (oak canopy > 0%), 2) some forest canopy but no oak canopy present (oak = 0% and non-oak forest > 0%), and 3) no forest canopy cover (open = 100%). These categories allowed me to distinguish between subplots located under or at the edge of oak canopy, under or at the edge of non-oak forest, and under no forest canopy (open). I also binned

both subplots and plots into three canopy density categories: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). In these categories, oak and non-oak forest percentages are summed together.

Understory types included: shrub, dense invasive, grass, and open/herb. Some plots and subplots included areas of lawn, gravel road, tree trunks and brush piles. These are areas where regeneration cannot take place. Consequently, any such plots or subplots were removed from the analysis. Invasive species found during the survey include Scotch broom (*Cytisus scoparius* (L.) Link), blackberry (*Rubus armeniacus* Focke [*Rubus discolor*]), ivy (*Hedera hibernica* (G. Kirchn.) Bean), and reed canary grass (*Phalaris arundinacea* L.). Except for Scotch broom, these species were individually present in very few plots. Therefore, Scotch broom was lumped with other shrubs due to their similar growth form, while the other invasive species, which create dense cover conditions, were lumped into their own "dense invasive" category. Scotch broom was also analyzed separately as its own category.

To create understory categories, I binned each plot and subplot into their dominant understory types. An understory type was considered dominant if it covered more than 60% of the plot or subplot area. For this analysis, Scotch broom, shrub and dense invasive were all considered "shrub." This resulted in four understory categories: shrub, grass, open/herb, and mixed (when no one understory type was >60%). At the plot level, only 5 plots were categorized as open/herb so these were removed from that analysis.

Statistical Analysis

I applied general linear mixed models to analyze relationships between seedling and sapling abundance and subplot, plot, and landscape characteristics. Mixed models account for the nested data structure of subplots within plots within oak woodlands. Dependent variables include: the quadratic mean adult tree DBH, total oak basal area per plot, seedling counts in subplots, and class 1 and 2 sapling counts in plots. Independent variables included woodland area, landscape urban cover, and plot and subplot understory and canopy estimates (Table 1).

Seedling counts for each subplot were tested against understory and canopy measures at the subplot level and landscape measures at the woodland level. In these models, both plot and woodland were included as random effects. Sapling and adult measures were tested against understory and canopy measures at the plot level and

TABLE 1. Direction and significance of linear mixed-effects models for seedling, young (class 1) sapling, and old (class 2) sapling abundance. Significance for all models was set at α ≤ 0.05. P-values of 0.1 or less are reported, n.s. indicates a p-value > 0.1. Sign indicates the direction of the relationship.

| Independent variables | | | Dependent variables | | | | | |
| | | | Seedlings | | Young (class 1) saplings | | Old (class 2) saplings | |
Scale	Variable	Description	Sign	p-value	Sign	p-value	Sign	p-value
Woodland	% Urban	>50% impervious (30 meter resolution land cover)	-	n.s.	-	0.06	+	n.s.
Woodland	Urban (categorical)	urban: > 40% , non-urban: < 40% urban cover	+	n.s.	-	0.05	+	n.s.
Woodland	Ft. Lewis (dummy)	1 = on Ft. Lewis, 0 = off Ft. Lewis	-	n.s.	+	0.08	+	n.s.
Plot	Total oak basal area (m^2)	Summed for each plot	+	0.07	-	0.07	-	<0.001
Plot	Quadratic mean DBH (cm)	$\sqrt{(\sum d_i^2)/n}$	+	n.s.	-	0.1	-	<0.0001
Plot/Subplot	% Oak canopy	*Q. garryana* canopy	+	0.05	-	n.s.	+	<0.0001
Plot/Subplot	% Open canopy	no tree canopy	-	<0.001	+	n.s.	-	<0.0001
Plot/Subplot	% Non-oak forest canopy	conifer or non-oak deciduous canopy	+	n.s.	-	n.s.	-	n.s.
Plot/Subplot	% Grass	no including lawn	+	<0.0001	-	n.s.	-	<0.0001
Plot/Subplot	% Open/Herb	Herbaceous, Fern, Moss, and Bare Ground	-	<0.0001	-	<0.001	-	n.s.
Plot/Subplot	% Shrub	eg. Snowberry, Indian Plum, Includes Scotch Broom	-	n.s.	+	0.001	+	<0.0001
Plot/Subplot	% Dense invasive	Himalayan Blackberry, Ivy, Reed Canary Grass	+	n.s.	-	n.s.	-	0.02
Plot/Subplot	% Scotch Broom		+	n.s.	+	<0.0001	+	<0.01
Plot/Subplot	% All shrub	Native shrub + Scotch broom + dense invasive	-	n.s.	+	0.01	+	<0.0001
Plot	Seedling total (count)	Sum of all subplots within one plot	n/a	n/a	+	<0.0001	-	n.s.
Plot	Class 1 sapling total (count)	Total count per plot	n/a	n/a	n/a	n/a	+	<0.0001

landscape measures at the woodland level. In these models, woodland was included as a random effect. Models using count data (e.g., seedling and sapling counts) were fit using the Laplace approximation and Poisson distribution (lme4 package, R 2.11.1 software). Models using continuous data (e.g., oak mean DBH) were fit by maximizing the restricted log-likelihood and the Gaussian distribution (nlme package, R 2.11.1 software). Significance for all models was set at α ≤ 0.05.

Results

A total of 128 10-m plots and 554 1-m plots were included in the final analysis, after removing all plots and subplots with unnatural (lawn, gravel road etc.) understory. Within these plots, adult oaks comprised over 70% of the total tree basal area surveyed. The next most dominant species was Douglas-fir (*Pseudostuga menziesii* (Mirb.) Franco) which accounted for 20% of the basal area. Remaining species each accounted for less than 3% total basal area measured, these included Pacific madrone (*Arbutus menziesii* Pursh), Oregon ash (*Fraxinus latifolia* Benth.), big leaf maple (*Acer macrophyllum* Pursh), red alder (*Alnus rubra* Bong.), and ponderosa pine (*Pinus ponderosa* C. Lawson).

Two variables, oak woodland area and a dummy variable indicating whether the site is located on JBLM, were not found to have any significant relationships to any of the dependent variables. I ran each of the models including the JBLM dummy variable and found that this did not change the significance or direction of any of the relationships except for the relationship between seedling abundance and landscape urban development. After including JBLM in the model, seedlings were negatively correlated with urban land cover. However, the majority of sites located off JBLM were significantly more urbanized than those on JBLM, making these two variables highly correlated. This high co-linearity, together with the fact that neither variable is significantly correlated to seedling abundance alone, suggests that this finding is spurious.

Effects of Canopy Cover

The data support my first hypothesis that seedlings are more abundant under forest canopy cover. Seedlings were more abundant with increasing amounts of oak canopy cover, and were less abundant with increasing amounts of open (non-forested) canopy (Table 1). Using canopy composition as a categorical variable showed that oak seedlings were least abundant under non-forest canopy (Figure 2). Comparing seedling abundance under closed, mixed and open canopy conditions again showed that abundance is lowest in open conditions (Figure 3). Oak seedling abundance appeared to peak under mixed canopy closure conditions, but this was
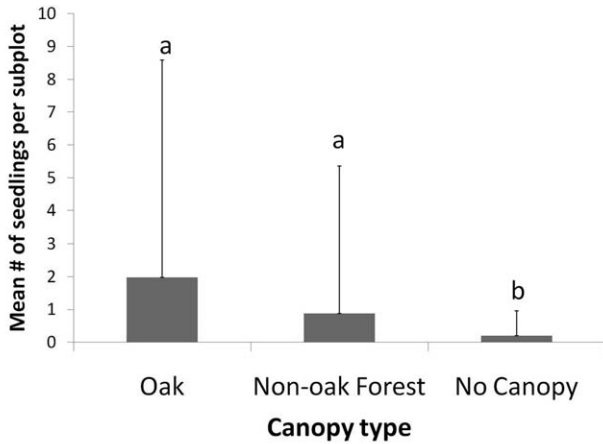
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Figure 2. Mean number of seedlings (+1 sd) by canopy type. Oak = some oak canopy present (oak canopy > 0%), non-oak forest canopy =some forest present, but no oak canopy present (oak = 0% and conifer + deciduous + shrub > 0%), and open = no forest canopy cover (open = 100%). Categories labeled with the same letter are not significantly different ($P > 0.05$).
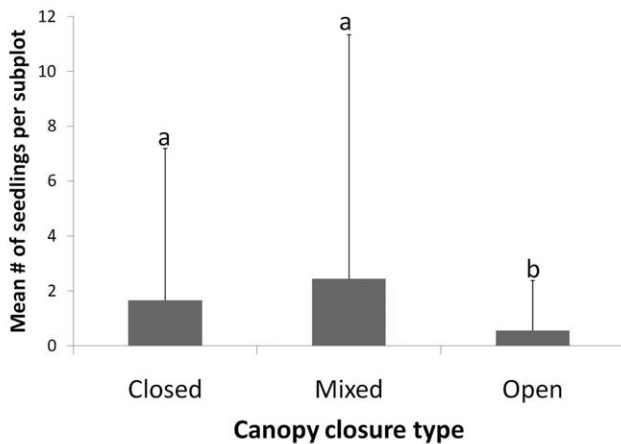

Figure 4. Mean number of old (class 2) saplings (+1 sd) by canopy closure type: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). Categories labeled with the same letter are not significantly different ($P > 0.05$).

Figure 3. Mean number of seedlings (+1 sd) by canopy closure type: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). Categories labeled with the same letter are not significantly different ($P > 0.05$).

Figure 5. Mean number of young (class 1) saplings (+1 sd) by canopy closure type: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). Categories labeled with the same letter are not significantly different ($P > 0.05$).

not significantly different from closed canopy. Similarly, old (class 2) saplings were positively correlated with percent oak canopy, negatively correlated with percent open canopy (Table 1), and least abundant in plots with open forest canopy (Figure 4). Young (class 1) saplings showed no relationship to canopy cover (Table 1, Figure 5).

Effects of Understory Type

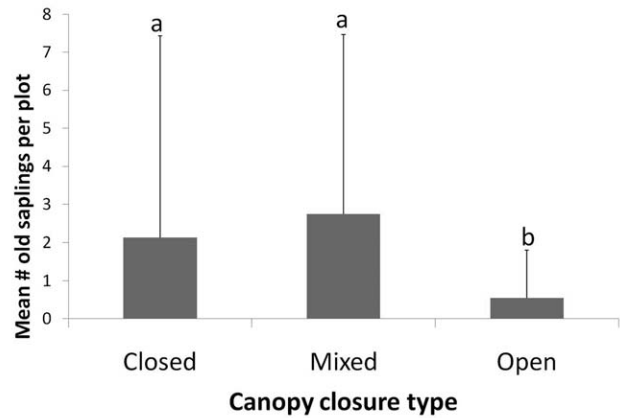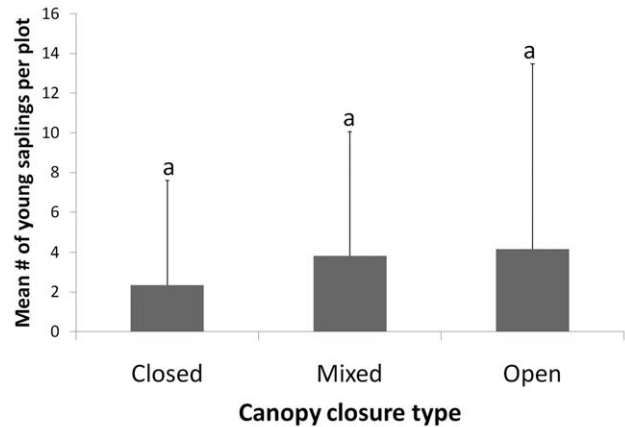The most prevalent understory types were shrub (including Scotch broom) and grass. Scotch broom alone

was a somewhat common understory component (73 subplots or 13%). Other invasive species were only present in a few subplots: blackberry (10 subplots), ivy (16 subplots), and reed canary grass (3 subplots). Scotch broom was not significantly related to seedling abundance but was positively correlated with young (class 1) and old (class 2) saplings abundance (Table 1). The dense invasive category was only present in 27 subplots, but was negatively correlated with old (class 2) saplings. However, it is questionable whether this sample is sufficient to identify valid relationships.

The data do not support my second hypothesis as seedling abundance differed between understory types.

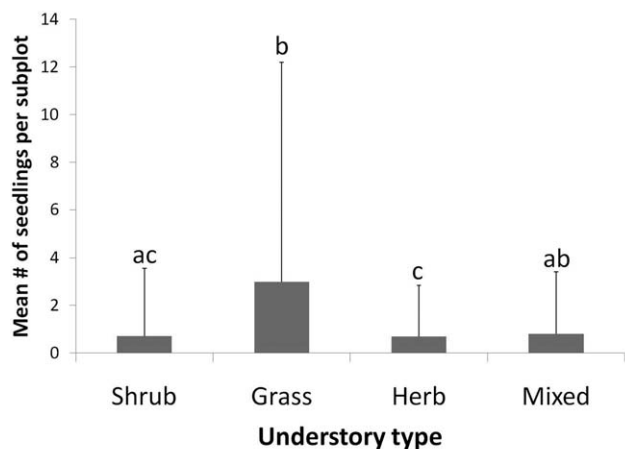Patterns of Urban Oregon White Oak Regeneration   187

Figure 6. Mean number of seedlings (+1 sd) dominant understory category. Categories labeled with the same letter are not significantly different ($P > 0.05$).
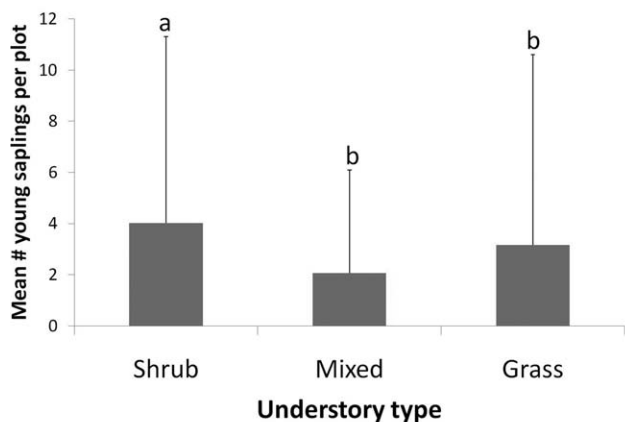

Figure 7. Mean number of young (class 1) saplings (+1 sd) by dominant understory category. Categories labeled with the same letter are not significantly different ($P > 0.05$).
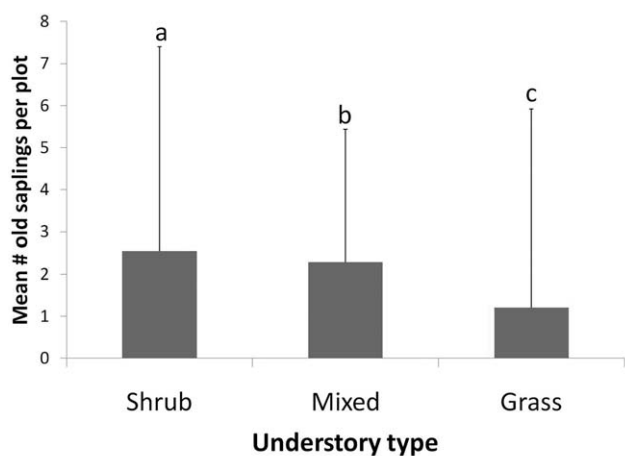

Figure 8. Mean number of old (class 2) saplings (+1 sd) by dominant understory category. Categories labeled with the same letter are not significantly different ($P > 0.05$).

Seedling abundance was strongly positively correlated with grass understory (Table 1), and seedlings were most abundant in grass-dominated and mixed subplots (Figure 6). In contrast, old (class 2) saplings were negatively correlated with grass. Abundance of both young (class 1) and old (class 2) saplings increased with increasing percent shrub cover (Table 1). In addition, both classes were most abundant in plots dominated by shrub cover (Figure 7 and 8). These results do not support my third hypothesis. While saplings did respond differently to understory conditions compared to seedlings, they showed a tighter relationship to disperser species habitat preferences than seedlings, as rodents are known to prefer shrub understory. Seedlings and saplings were all negatively correlated with open/herb understory, although this relationship was only significant for seedlings and young (class 1) saplings (Table 1).

Effects of Urban Development

Urban development, as either a continuous or categorical variable, was not significantly related to any of the dependent variables measured, except young saplings. There was a marginally significant, negative relationship between young (class 1) sapling abundance and percent urban land cover (Table 1, $P = 0.06$). Classifying each woodland into either urban (> 40% urban cover) or non-urban (< 40% urban cover) demonstrated that young (class 1) oak saplings were significantly less abundant in oak woodlands surrounded by more than 40% urban cover (Figure 9).
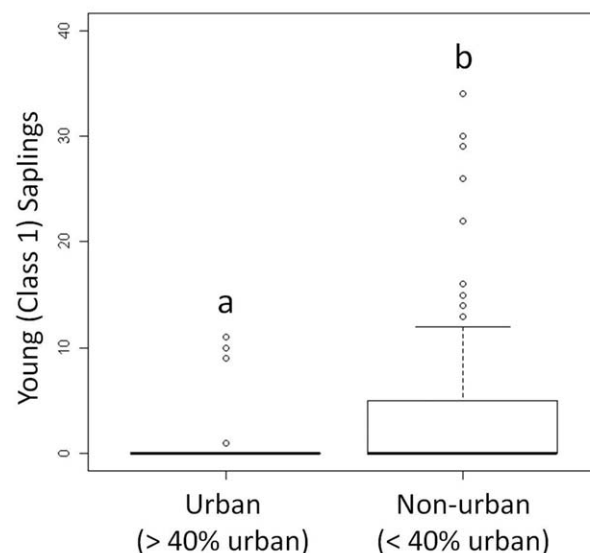

Figure 9. Comparison of young (class 1) sapling abundance in urban and non-urban oak woodlands. Categories labeled with different letters are significantly different ($P = 0.05$).

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Discussion

Effects of Canopy Cover

Recruitment patterns within oak stands appear to change overtime. Oak seedlings were most abundant under oak canopy (Table 1, Figure 2), but older (class 2) saplings were less abundant with increasing adult oak basal area and DBH (Table 1). One interpretation of these findings is that although the majority of acorns germinate beneath adult trees, survival of seedlings is lower in these areas. Brudvig and Asbjornsen (2005) found the highest abundance of *Quercus alba* seedlings within existing oak stands, but noted low increases in height and basal area in these areas compared to seedlings located in canopy gaps. A lack of regeneration within existing oak stands and apparent suppression of conspecifics by adult trees has been documented in other oak systems as well (Callaway and Davies 1998). Density-dependent mortality is common in plant species and seed dispersal away from parent trees is seen as an important adaptation to escape this mortality (Janzen 1970).

Beyond the oak canopy, seedlings were significantly more abundant under or near forest canopy than in non-forested areas (Figure 2). Regan (2001) also found that *Q. garryana* seedlings on JBLM were most abundant under oak, then conifer canopy and least abundant in open areas. Three factors may lead to a lack of seedlings in non-forested areas: 1) reduced dispersal to these areas, 2) poor environmental conditions for seedling emergence in these areas, and 3) heavy shoot herbivory in these areas. The first explanation is supported by several studies reporting that jays and rodents prefer to cache acorns under forest cover (Fuchs et al. 2000b, Gomez 2003, Pons and Pausas 2007, Gomez et al. 2008). The second explanation is not supported by a study by Fuchs et al. (2000a), who demonstrated that experimental acorn plantings survived and produced seedlings in most habitat types regardless of percent cover overstory vegetation. Work by Callaway (1992) supports the third explanation, which found very low survival of *Q. douglasii* seedlings in open grassland habitats compared to shrub habitats, primarily due to shoot herbivory. Based on these other studies, it is evident that additional experimental studies are needed to determine the relative importance of dispersal, environmental conditions, and herbivory as drivers of seedling abundance in this system.

Effects of Understory Type

The finding that seedlings were more abundant in grass- and mixed- understory types, rather than shrubs

(Figure 6), may be related to seed predation behavior of dispersers and other animals. Several studies have found that rodent seed predation is heavier in areas with dense shrub cover (Smit et al. 2001, Kollmann and Buschor 2002, Muñoz and Bonal 2007, Perez-Ramos and Marañón 2008), and is generally reduced in open habitats (Hulme 1998). Fuchs and others (2000b) found that acorn predation on *Q. garryana* tended to be low in herb and high in shrub understory. Callaway (1992) found that acorn predation was the primary cause of mortality for *Q. douglasii* in shrublands, but shoot herbivory was more common in open grasslands.

In contrast to seedlings, the high abundance of both classes of saplings in areas with higher shrub cover suggests that shrub cover may favor regeneration (Figures 7 and 8). Similar results were found in a meta-analysis of shrubs as nurse plants in Spain, where Gomez-Aparicio et al. (2004) found that shrubs had a positive effect on woody plant seedling growth and survival for 18 tree species and that *Quercus* spp. showed the greatest positive response. Other studies have documented that shrubs facilitate oak recruitment in *Quercus agrifolia* (Callaway and Davis 1998) and *Q. douglasii* (Callaway 1992) in California and *Q. humilis* in France (Rousset and Lepart 1999).

Shrubs potentially facilitate oak regeneration through two primary mechanisms: 1) protecting seedlings from herbivores and 2) improving microclimatic conditions by providing shade. Oak leaves are particularly nutritious browse for deer and may experience heavy grazing pressure from herbivores (Larsen and Morgan 1998). Rousset and Lepart (1999) found that shrubs effectively protected oak seedlings from sheep herbivory, thereby increasing survival and growth. Callaway (1992) found that experimentally excluding herbivores improved *Q. douglasii* survival somewhat, but that excluding herbivores and providing artificial shade was necessary to increase seedling survival to levels comparable to those in shrub habitat. In contrast, Fuchs and others (2000a) found that while desiccation is a significant source of *Q. garryana* seedling mortality, there was no relationship between shade cover and desiccation mortality for experimentally planted seedlings.

My findings suggest that while acorns in grasslands may experience lower seed predation and therefore have a higher chance of germinating, seedlings in shrub habitat have a higher chance of surviving to the sapling stage. Gomez-Aparicio and others (2004) argue that shrub cover, which is commonly removed as a forest competitor, may actually enhance natural forest regeneration in the Mediterranean. While more experimental

work is needed, my results suggest that shrubs may be important for *Q. garryana* regeneration as well. In this study, Scotch broom, an invasive species and the subject of significant removal efforts in this region, was included as a "shrub." Both young and old saplings were more abundant in plots with Scotch broom, suggesting that it may provide benefits similar to other native shrubs in the region. However, managers will need to weigh the benefits Scotch broom potentially provides to oak regeneration against the costs it incurs to other native species in the oak ecosystem.

Effects of Urban Development

Young sapling abundance was significantly lower in urban areas (Figure 9) possibly due to concomitant differences in urban herbivore populations. Deer often reach high densities in urbanized regions due to reduced predation and abundant nutritious browse (Etter et al. 2002, Bender et al. 2004). High deer densities can cause significant damage to vegetation through overgrazing (Stromayer and Warren 1997, Horsley et al. 2003, Côtè et al. 2004). In addition to deer, eastern cottontail rabbits (*Sylvilagus floridanus*) spread rapidly throughout western Washington after their introduction in 1927 (Dalquest 1941). Although little is known about urban populations of *S. floridanus* in the study area, this species has adapted well to fragmented landscapes in Massachusetts (Smith and Litvaitus 2000) and is another potentially unchecked herbivore.

Urban areas have very different climatic, hydrologic and chemical characteristics compared to rural areas (McDonnell et al. 1997), so it is possible that these microclimatic conditions adversely affect seedling survival. Urban soils are often drier due to both increased temperatures in urban landscapes and increased water runoff due to impervious surfaces (Pickett and Cadenasso 2009). These changes in soil moisture may reduce seedling survival and subsequent transition to the sapling stage, given that desiccation is one of the most common causes of oak mortality (Fuchs et al. 2000a, Johnson et al. 2002). It is possible that a combination of local environmental changes and altered herbivore pressure result in the reduced sapling abundance in urban areas observed in this study. Lastly, while the areas included in this study all had natural understory and unmowed grass, it is possible that managers periodically mow tall grasses in urban sites, which would significantly reduce sapling survival.

The lack of a relationship between older saplings and landscape urban cover may be due to the accumulated effects of urban development over time. These effects may not have been significant when the older saplings were developing, but have become more intense in recent years. Alternatively, urban environments may be more favorable, or less detrimental, to sapling survival in later life history stages. For example, residential and commercial development may increase edge habitat, which could benefit oak saplings by providing greater access to sunlight. More research into sapling growth and survival in urban landscapes is needed to understand these patterns.

Human and Management Impacts

All of the sites included in this study have been heavily used and managed by people for decades, if not centuries. The urban sites located off of JBLM are all in public parks, where they experience different levels of recreational use as well as vegetation management. Conversations with park managers indicated that the understory of the areas included in this study was not actively managed. Forestry officials on JBLM do actively manage for oak habitat, including periodic burning, selective thinning, and mowing Scotch broom. In addition, areas of JBLM experience significant disturbance from military training activities. None of the study sites were burned or mowed immediately prior to conducting the vegetation surveys. However, training activities were ongoing during the survey. These activities clearly have a potentially strong influence on oak stand structure and cannot be discounted.

Regan (2001) found that burning significantly reduces the number of oak saplings between 0.1 and 10 cm DBH and has some beneficial effects on seedling growth. In this study, I found no difference in seedling abundance on or off JBLM (Table 1). This either suggests that burning is not applied widely enough on JBLM to raise the average seedling abundance, or that conditions off JBLM somehow compensate for a lack of burning. Alternatively, my sample may not be large enough to capture real differences, because seedling abundance is highly variable. Regan (2001) notes that the relationship between conifer canopy cover and seedling abundance is possibly obscured by prescribed burning, which also influences the behavior of seed predators. Here, I found the same positive relationship between canopy cover and seedling abundance (Figure 2) regardless of the application of burn management.

Similarly, if burning on JBLM reduces sapling abundance, then I would expect to see a higher abundance of saplings in the unburned sites *off* JBLM. Instead, young saplings are significantly *less* abundant in unburned, urban sites (Figure 9), and older sapling abundance is

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not significantly different (Table 1). Finally, controlling for location on and off JBLM does not change the observed relationships between canopy cover and understory for any oak age class.

Conclusions and Management Implications

Understanding the relationship between landscape condition, habitat structure, seed dispersal and seedling recruitment can improve oak management practices. Protecting the long-term persistence of plant populations requires that existing stands adequately regenerate and that plant propagules are able to disperse and colonize new habitat as it becomes available. At the landscape level, understanding the effects of urban development on oak regeneration will help managers and urban planners understand whether current oak protection ordinances are adequately maintaining regeneration processes, or only protecting existing adult trees in developing regions. While seedlings are most abundant under existing oak canopy, regeneration in existing oak stands is often suppressed (Calloway 1992). With *Q. garryana*, dispersal beyond the oak canopy is directed to areas with forest cover. Subsequently, managers may be able to encourage oak regeneration and expansion of oak habitat by maintaining forest cover adjacent to oak stands.

At the site level, manipulating habitat structures can be an effective way to attract seed dispersers and accelerate plant succession in restoration efforts (Robinson and Handel 2000, Gomez-Aparicio et al. 2004, Herrera and Garcia 2010). Peter and Harrington (2002) found that Oregon white oaks with less crown contact with other trees produce more acorns and that urban oak trees produce on average as many acorns as non-urban trees. Increasing crop size through site level management activities may attract more animal dispersers. Enhancing natural dispersal may be preferable to planting nursery grown seeds and seedlings because nursery stock may not be genetically adapted to the location and may have lower genetic diversity (Robinson and Handel 2000). In addition, harnessing free dispersal services of animal dispersers is significantly less expensive than hiring humans to distribute and plant oak acorns (Hougner et al. 2006). In areas where seedlings are abundant, protecting existing seedlings from herbivory may be a more cost effective approach to restoration than planting acorns or purchasing nursery seedlings. In addition, maintaining shrub cover may facilitate oak seedling survival and oak recruitment in grassland environments (Gomez-Aparicio et al. 2004). Planting oak seedlings or targeting management of naturally occurring seedlings in shrub cover could improve restoration success and reduce maintenance costs.

Acknowledgements

Literature Cited

Acacio, V., M. Holmgren, F. Moreira, and G. M. J. Mohren. 2010. Oak persistence in Mediterranean landscapes: the combined role of management, topography, and wildfires. Ecology and Society 15(4): 40.[online] URL:http://www.ecologyandsociety.org/vol15/iss4/art40/

Alberti, M. A., J. M. Marzluff, P. Waddell et al. (2006) Modeling interactions among urban development, land-cover change, and bird diversity. NSF Final Report BE/CNH 0120024.

Alig, R. and E. White. 2007. Protections of forestland and developed land areas in Western Washington. Western Journal of Applied Forestry 22:29-35.

Asquith, N. M., J. Terborgh, A. E. Arnold, and C. M. Riveros. 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. Journal of Tropical Ecology 15:229-235.

Bender, L. C., J. C. Lewis, and D. P. Anderson. 2004. Population ecology of Columbian black-tailed deer in urban Vancouver, WA. Northwestern Naturalist 85:53-59.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506-519.

Browers, M. A., and B. Breland. 1996. Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. Ecological Applications 6:135-1142.

Brudvig, L. A., and H. Asbjornsen. 2005. Oak regeneration before and after initial restoration efforts in a tall grass oak savanna. American Midland Naturalist 153:180-186.

Callaway, R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology 73:2118-2128.

Callaway, R. M., and F. W. Davies. 1998. Recruitment of *Quercus agrifolia* in Central California: the importance of shrub-dominated patches. Journal of Vegetation Science 9:647-656.

Christian, C. E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature 413:635-639.

Côtè, S. D., T. P. Rooney, J-P Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.

Dalquest, W. W. 1941. Distribution of cottontail rabbits in Washington State. Journal of Wildlife Management 5:408-411.

Etter, D. R., K. M. Hollis, T. R. Van Deelen, D. R. Ludwig, J. E. Chelsvig, C. L. Anchor, and R. E. Warner. 2002. Survival and movements of white-tailed deer in suburban Chicago, Illinois. Journal of Wildlife Management 66:500-510.

Fisher, A. P., and J. C. Bliss. 2008. Behavioral assumptions of conservation policy: conserving oak habitat on family-forest land in the Willamette valley, Oregon. Conservation Biology 22:275-283.

JBLM soil series [Shapefile]. JBLM, WA: Joint Base Lewis Mc-Chord Public Works Forestry Branch, date unknown.

Fuchs, M. A., P. G. Krannitz, A. S. Harestad. 2000a. Factors affecting emergence and first-year survival of seedlings of Garry Oaks (*Quercus garryana*) in British Columbia, Canada. Forest Ecology and Management 137:209-219.

Fuchs, M. A., P. G. Krannitz, and A. S. Harestad. 2000b. Dispersal of Garry oak acorns by Steller's jays. Proceedings of Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15–19 Feb., 1999. Volume One. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 490pp.

Fuchs, M. A. 2001. Towards a Recovery Strategy for Garry Oak and Associated Ecosystems in Canada: Ecological Assessment and Literature Review. Technical Report GBEI/EC-00-030. Environment Canada, Canadian Wildlife Service, Pacific and Yukon Region.

Garcia, D., and J. R. Obesco. 2003. Facilitation by herbivore-mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. Ecography 26:739-750.

Gomez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573-584.

Gomez, J. M., C. Puerta-Pinero, E. W. Schupp. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. Oecologica 155:529-537.

Gomez-Aparicio, L., R. Zamora, J. M. Gomez, J. A. Hodar, J. Castro, and E. Baraza. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128-1138.

Herrera, J. M., and D. Garcia. 2010. Effects of forest fragmentation on seed dispersal and seedling establishment in orinthochorous trees. Conservation Biology 24:1089-1098.

Horsley, S. B., S. L. Stout, and D. S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98-118.

Hougner, C., J. Colding, and T. Søderqvist. 2006. Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden. Ecological Economics 59:364-374.

Howe, H. F., and M. N. Mitiri. 2000. No question: seed dispersal matters. Trends in Ecology and Evolution 15:434-436.

Hulme, P. E. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. Perspectives in Plant Ecology, Evolution and Systematics 1:32-46.

Janzen, D. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104:501-528.

Johnson, P., S. Shifley, and R. Rogers. 2002. The Ecology and Silviculture of Oaks. CAB International, Cambridge, MA.

Kollmann, J., and M. Buschor. 2002. Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. Plant Ecology 164:249-261.

Larsen, E. M., and J. T. Morgan 1998. Management recommendations for Washington's priority habitats: Oregon White Oak Woodlands. Washington Department of Fish and Wildlife, Olympia, WA. 37pp.

MacDougall, A. S., B. R. Beckwith, and C. Y. Maslovat. 2004. Defining conservation strategies with historical perspectives: a case study from a degraded oak grassland ecosystem. Conservation Biology 18:455-465.

McDonnell, M. J., S. T. A. Pickett, P. Groffman, P. Bohlen, R. V. Pouyat, W. C. Zipperer, R. W. Parmelee, M. M. Carreiro, and K. Medley. 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems 1:21-36.

Moore, J. E., and R. K. Swihart. 2007. Importance of fragmentation-tolerant species as seed dispersers in disturbed landscapes. Oecologia 151:663-674.

Muñoz, A., and R. Bonal. 2007. Rodents change acorn dispersal behavior in response to ungulate presence. Oikos 116:1631-1638.

Pérez-Ramos, I. M., and T. Marañón. 2008. Factors affecting post-dispersal seed predation in two coexisting oak species: microhabitat, burial and exclusion of large herbivores. Forest Ecology and Management 255:3506-3514.

Peter, D., and C. Harrington. 2002. Site and tree factors in Oregon white oak acorn production in western Washington and Oregon. Northwest Science 76:189-201.

Pickett, S. T. A., and M. L. Cadenasso. 2009. Altered resources, disturbance, and heterogeneity: a framework for comparing urban and non-urban soils. Urban Ecosystems 12:23-44.

Pierce County Soils [Shapefile]. Olympia, WA: Washington State Department of Natural Resources (WDNR), 2005.

Pons, J., and J. G. Pausas. 2007. Acorn dispersal estimated by radio-tracking. Oecologica 153:903-911.

Regan, A. C. 2001. The effects of fire on woodland structure and regeneration of *Quercus garryana* at Fort Lewis, Washington. M.S. Thesis, University of Washington, Seattle.

Robinson, G. R., and S. N. Handel. 2000. Directing spatial patterns of recruitment during an experimental urban woodland reclamation. Ecological Applications 10:174-188.

Rousset, O., and J. Lepart. 1999. Shrub facilitation of *Quercus humilis* regeneration in succession on calcareous grasslands. Journal of Vegetation Science 10:493-502.

Russo, S. E., S. Portnoy, and C. K. Augspurger. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecology 87:3160-3174.

Ryan, L. A., and A. B. Carey. 1995. Distribution and habitat of the Western gray squirrel (*Sciurus griseus*) on Ft. Lewis, Washington. Northwest Science 69:204-216.

Shochat, E., S. B. Lerman, M. Katti, and D. B. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. The American Naturalist 164:232-243.

Smit, R., J. Bokdam, J. den Ouden, H. Olff, H. Schot-Opschoor, and M. Schrijvers. 2001. Effects of introduction and exclusion of large herbivores on small rodent communities. Plant Ecology 155:119-127.

Smith, D. F., and J. A. Litvaitus. 2000. Foraging strategies of sympatric lagomorphs: implications for differential success in fragmented landscapes. Canadian Journal of Zoology 78:2134-2141.

Stromayer, K. A. K., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227-234.

Thurston County Soils [Shapefile]. Olympic, WA: Thurston County Geodata Center, 1998.

Vigallon, S. M., and J. M. Marzluff. 2005. Abundance, nest sites, and nesting success of Steller's Jays along a gradient of urbanization in Western Washington. Northwest Science 79:22-27.

Western Regional Climate Center (WRCC). 2010. Washington climate summaries. National Oceanic and Atmospheric Administration, Reno, NV. Available online at http://www.wrcc.dri.edu/summary/climsmwa.html (accessed 3 October, 2010).

Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology. 15:523-533.