Implications of Urbanization and Climate Change for Oregon White Oak (*Quercus garryana*) Regeneration, Planning, and Management in the Pacific Northwest.

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Abstract

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Land-cover and climate change pose significant challenges to ecological planning and management. Ecological responses to these changes are mediated by the interactions between landscape structure, biodiversity, and ecosystem function. I use a case study of Oregon white oak in the rapidly urbanizing coastal Pacific Northwest to explore these interactions and their implications for planning.

Biodiversity changes dramatically as urban development intensifies. Yet the subsequent impacts on ecological functions remain relatively unexplored. I hypothesize that urbanization alters the community composition of acorn-dispersing animal species, and that this, in conjunction with fine-scaled habitat and foraging interactions, will generate unique dispersal and regeneration patterns in urban oak woodlands. I tracked the dispersal of individual acorns directly to test whether dispersal differs in urban and non-urban landscapes and used experimental acorn plantings and observations of seedling and sapling abundance to test whether urbanization influences later stages of oak regeneration. I found that more acorns were consumed and dispersal distances were shorter in urban oak woodlands making acorn dispersal services

inferior to those in non-urban landscapes. Seedling production and abundance did not differ between urban and non-urban sites, although young saplings were less abundant in urban oak woodlands. Understanding the effects of landscape patterns on regeneration processes is essential for learning how to manage urban oak ecosystems.

Due to their complexity, understanding how ecological systems will respond to climate change is highly uncertain. I evaluate potential climate impacts on Oregon white oak in the Willamette Valley using a range of information sources to identify consensus, uncertainty, and knowledge gaps in our understanding of oak vulnerability. Based on this assessment, I develop resource response scenarios to incorporate irreducible uncertainty directly into the planning process and identify flexible and robust adaptation strategies for oak management.

As land-cover and climate changes intensify, ecological planning practice must expand to include human-dominated landscapes, such as urbanizing regions, productively. In addition, management plans must be flexible and robust to future uncertainties. Understanding the ecological implications of these changes, and developing appropriate management and adaptation strategies, are essential tasks for ecological planners in the next century.

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INTRODUCTION

In the past decades, ecologists' evolving understanding of ecosystem structure and function (Gunderson, 2002), coupled with a growing awareness of the increasing pace and scale of anthropogenic global change (Vitousek, 1994), have challenged critical elements of traditional ecological planning (Bengtsson et al., 2003; Hannah et al., 2002). Specifically, ecological planning faces two significant challenges in the coming century. First, the field will need to expand in scope to incorporate human-dominated ecosystems more explicitly into ecological networks (Kostyack et al., 2011; Lindenmayer and Franklin, 2002). Understanding how human activities, such as urban development, alter fundamental ecological processes and how ecosystems respond and adapt to these changes, is essential for managing biodiversity and ecosystem services in human-dominated landscapes. Second, it is becoming increasingly clear that, due to climate change, the only certainty for ecological management in the future is change (Millar et al., 2007; Stein et al., 2013). Both land-cover and climate change have and will continue to have significant impacts on biodiversity (McDonald et al., 2013; Staudinger et al., 2013) with substantial, but highly uncertain, cascading effects on community structure and ecosystem function (Gilman et al., 2010). Traditional planning approaches that aim to recreate and maintain ecosystems based on reference conditions from the past will not be able to meet the evolving needs of ecological systems in the future (Stein et al., 2013).

To meet these challenges, ecological planning must adapt. Incorporating human-dominated landscapes into ecological networks will require that planners have a better mechanistic understanding of how landscape changes, such as urbanization, influence ecosystem functions and processes. Building such knowledge requires using experimental methods to collect empirical data measuring the functions and processes of human-dominated ecosystems. Planning for an uncertain future requires openness to seeking out both consensus and disagreement in expected ecological responses to future change. Uncertainty found through disagreement and knowledge gaps must be incorporated into the planning process explicitly to avoid developing plans and strategies that rely on a narrow view of the future. To address both these challenges, planning approaches must encourage experimentation, creativity, and flexibility. In addition, our understanding and definition of ecological systems will need to evolve to accommodate novel and dynamic species assemblages and ecological processes (Pickett et al., 2011).

Complexity, Urbanization, Biodiversity and Ecosystem Function

Over the last century, urban regions have grown at an increasingly rapid rate. Researchers project that between 2000 and 2050, urban regions will expand by two to five times in area depending on per capita land use (Angel et al., 2010). This rapid urban growth will have significant consequences for local, regional and global ecosystem dynamics (McDonald et al., 2013; McPhearson et al., 2013). Urbanization alters both biotic and abiotic conditions directly by clearing and fragmenting native vegetation and indirectly by altering temperature, hydrology, productivity, noise, and pollution levels (Grimm et al., 2008; Pickett et al., 2011). Many studies have found that urban development leads to a reduction in native species richness and increased dominance of non-native, urban-adapted species (Blair, 1996; Marzluff, 2005; McDonald et al., 2013; McKinney, 2008). In addition, urban ecological communities often have reduced species evenness as a small number of species dominate total biomass (Blair, 1996; Grimm et al., 2008;

Shochat et al., 2006). The process of replacing native species with non-native, urban-adaptive species has been termed “biotic homogenization” and represents a significant threat to global biodiversity conservation (McKinney, 2006). While an increasing number of studies have documented systematic changes to species composition across urban regions, the consequences of these changes for ecosystem function remain relatively unexplored.

Complexity and hierarchy theory are central to understanding how biodiversity, landscape structure and ecosystem function interact (Levin, 1998; O’Neill et al., 1989; Urban et al., 1987). Complex adaptive systems, such as ecosystems, are made up of tightly interacting, self-organizing, subgroups or components loosely linked together with other components that operate across multiple spatial and temporal scales. Feedbacks within complex systems can reinforce chance events and lead to nonlinear dynamics. Consequently, complex systems can evolve in many different directions depending on accidents of history, local conditions, and changes in critical individual components (Levin, 1998). Hierarchy theory provides a framework for decomposing complex systems based on spatial and temporal scale. Actors and processes that operate at similar spatial and temporal scales form tightly interconnected modules or components which are nested within components that operate at larger scales. Components operating at finer scales, such as the presence or absence of particular species and their behaviors, provide the biotic potential or mechanisms driving processes at the focal scale (O’Neill et al., 1989). Broader-scale constraints, such as climate or habitat composition, provide the boundary conditions within which components at lower levels interact (Urban et al., 1987).

Based on hierarchy theory, ecological structure and function are connected by reciprocal feedback loops that operate both within and across scales (O’Neill et al., 1989). Changes to landscape structure can alter the presence, absence and abundance of species and lead to significant functional changes within an ecosystem (Folke et al., 2004). These alterations can be particularly dramatic when the removal or addition of a species creates cascading effects in food web and trophic structure (Faeth et al., 2005). A salient example is the removal of keystone predators, which can lead to the release of herbivores and a subsequent reduction in vegetation biomass (Folke et al., 2004; Ripple et al., 2001). However, shifts in animal community composition can lead to more subtle changes in plant community structure and function by altering the early stages of plant regeneration. Specifically, changes to seed disperser and herbivore populations have significant implications for the spatial distribution and abundance of plant populations (Nathan and Muller-Landau, 2000). Seed dispersal influences both where new plant individuals will establish and seed germination and survival success (Howe and Miriti, 2004; Janzen, 1970; Levin et al., 2003). For animal-dispersed seeds, the behavior and habitat preferences of animal seed dispersers interact with the spatial structure of the landscape to produce observed patterns of seed deposition (Russo et al., 2006). As a result, changes to the animal disperser community can lead to shifts in plant community composition as some seeds are no longer dispersed or may be dispersed to different locations (Caves et al., 2013; 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).

It is clear that ecosystem structure and function are strongly influenced by landscape context (Turner, 1989). Yet, our empirical knowledge of ecosystem function is largely based on studies conducted within large protected areas (Martin et al., 2012). This limited view of ecosystems is problematic given the prevalence and extent of anthropogenic land-cover change (Vitousek et al., 1997). While large reserves will continue to be important, we need a better understanding of how small protected areas as well as the human-dominated "matrix," or landscape surrounding protected areas, contribute to ecological networks (Bengtsson et al., 2003; Franklin and Lindenmayer, 2009; Kostyack et al., 2011). In addition, ecologists have a limited understanding of the mechanisms linking anthropogenic land-cover change to observed changes in ecosystem structure (Shochat et al., 2006) and the consequences of these changes for ecological function. A more mechanistic understanding of ecological processes in human-dominated landscapes is needed to both inform management of these systems and to evaluate their ecological contribution to larger ecological networks.

By altering the structure of the landscape, urbanization leads to changes in community composition, which subsequently alter ecosystem functions, which can, in turn, feedback to generate changes in community composition and landscape structure. Urbanization is known to create major changes to food web structure including the loss of top predators and increased abundance and consistency of food resources (Faeth et al., 2011). Structural changes driven by urban development have important implications for plant regeneration processes in particular. For example, the loss of large predators and the introduction of abundant and nutritious foliage has led to increases in deer populations in many suburban communities, placing significant pressure on forest seedlings and impeding forest regeneration (Côté et al., 2004). Reduced predation pressure and consistent food provision has changed seed consumption behavior of squirrels in urban Virginia (Bowers and Breland, 1996). Lastly, by altering the physical structure of the landscape, urban development could limit animal-mediated seed dispersal if animal dispersers are either not present or are unwilling to travel through developed areas (Marzluff and Ewing, 2001; Root and Schneider, 2006; Trakhtenbrot et al., 2005).

Complexity, Urbanization and Oregon White Oak Regeneration

The Puget Sound region in western Washington State has experienced significant urban expansion in recent decades (Alberti et al., 2004; Alig and White, 2007), leaving numerous forest remnants embedded in an urban landscape. These landscape changes are a particular concern for increasingly rare Oregon white oak (*Quercus garryana*) woodlands. This species is the only native oak species in Washington State and therefore represents a unique element of the region's biodiversity. *Q. garryana* plays a particularly important ecological role because acorns provide a critical food resource for a wide range of animals, including the state-threatened western gray squirrel (*Sciurus griseus*). Local governments and conservation groups have expended significant effort to protect oak woodlands in both urban and non-urban areas (Larsen and Morgan, 1998). However, these efforts focus solely on adult trees with little knowledge of whether regeneration within protected stands is sufficient to sustain the population.

Seed dispersal is a critical stage of the regeneration process with significant effects on plant community structure, dynamics and species composition (Levin et al., 2003). Seed dispersal dynamics influence range expansion, adaptation to climate change, re-colonization of unoccupied habitat, and the spread of invasive species (Trakhtenbrot et al., 2005). For plants that depend on animals for dispersal, research has demonstrated that changing landscape structure can alter seed dispersal patterns and processes by altering the distribution and abundance of animal dispersers (Markl et al., 2012; McConkey et al., 2012). Several studies have found that fragmentation alters dispersal processes (Battaglia et al 2008, Spiegel and Nathan 2007, Bacles 2006) and others hypothesize that urban development limits dispersal with consequences for plant adaptation to climate change (Root and Schneider, 2006; Schloss et al., 2012). Loss of dispersal services may have negative consequences for plant community structure and genetic diversity, because plant recruitment and survival are higher when seeds are dispersed farther from the parent tree (Janzen, 1970; Levin et al., 2003).

Q. garryana acorns rely on a comparatively small number of animal species for dispersal (Larsen and Morgan, 1998). The key species mediating these processes are native Steller's jays (*Cyanocitta stelleri*), native western gray squirrels (*Sciurus griseus*), and non-native eastern gray squirrels (*Sciurus carolinensis*). Urban development is known to alter the distribution and abundance of all these species in western Washington (Ryan and Carey, 1995; Vigallon and Marzluff, 2005). By altering the composition of the seed-dispersing animal community, urbanization may have a significant impact on dispersal services including how many seeds are dispersed, how far seed are dispersed, where seeds are taken, and what proportion are consumed.

The fact that multiple species can provide dispersal services may be important for oak resilience to fragmentation and urban development. This is because even if two species perform similar functions, those species may operate at different spatial or temporal scales and/or may respond to disturbances differently (Elmqvist et al., 2003; Peterson et al., 1998). In the case of *Q. garryana*, each of the seed dispersers responds differently to urbanization. Western gray squirrels are not known to occupy forest patches in urban areas (Ryan and Carey, 1995), while 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). As a result, if eastern gray squirrels and jays are able to replace the dispersal functions lost by western gray squirrels in urban landscapes, then this particular stage of oak regeneration may be resilient to urban effects. Alternatively, because eastern gray squirrels are not native to this system, their seed dispersal services may be inferior or even harmful compared to services provided by western gray squirrels. A study comparing the dispersal behaviors of red (*Tamiasciurus hudsonicus*) and gray squirrels (*Sciurus carolinensis*) in the eastern United States concluded that the species provide unequal dispersal benefits and that red squirrels, whose range is expanding, would not be able to compensate for the lost dispersal services of the gray squirrels, whose range is contracting (Goheen and Swihart, 2003). In contrast, Moore and Swihart (2007) found that fox squirrels (*Sciurus niger*), which are tolerant of fragmentation, may be able to effectively replace the dispersal services of gray squirrels, which are intolerant of fragmented landscapes.

In addition to changing the types of animals available to disperse seeds, altered community and habitat conditions in urban landscapes may have an impact on dispersal behavior. Previous studies of foraging dynamics have found higher seed removal rates in urban landscapes, potentially due to a higher density of foraging individuals (Bowers and Breland, 1996; Shochat et al., 2004a). Eastern gray squirrels occur at higher densities in suburban and urban parklands compared to non-urban areas (van der Merwe et al., 2005). An increased abundance of seed-dispersing individuals often increases seed removal rates (Carlo and Morales, 2008; Hopewell et al., 2008), suggesting that removal rates could be higher in urban fragments. Eastern gray squirrels tend to remove acorn embryos to prolong storage through winter, and so increased numbers of eastern gray squirrels are likely to result in higher predation rates (Fuchs et al., 2000). Finally, urban development potentially influences the amount and spatial arraignment of forest cover (Goheen et al., 2003), foraging competition (Hopewell et al., 2008), and predation risk (Bednekoff, 2007) which in turn affect foraging and caching behavior, ultimately leading to altered spatial patterns of seed dispersal.

Incorporating Complexity, Uncertainty, and Climate Change into Ecological Planning

Climate is a fundamental driver of ecological processes such as ecosystem productivity, hydrologic cycles, wildfire regimes, snow pack formation and more (Grimm et al., 2013). Changes to these processes have significant implications for ecological structure and biodiversity. At large spatial and temporal scales, climate is one of the most important determinants of species distribution (Grinnell, 1917; Pearson and Dawson, 2003). Fossil records show that species have historically migrated long distances to track changing climate conditions (Davis and Shaw, 2001; Jacobson Jr et al., 1987) and observations over the last few decades indicate that species are already moving in response to recent anthropogenic climate change (Chen et al., 2011; Parmesan, 2006; Walther et al., 2002). Changes to species composition and ecosystem processes can lead to dramatic shifts in ecosystem state as complex interactions within and across scales create positive feedback loops that reinforce structural changes (Folke et al., 2004; Grimm et al., 2013). Indeed, due to climate change, 5-20% of the land area within the United States is projected to experience a shift in vegetation biome type (Gonzalez et al., 2010).

These dramatic projected changes to ecological structure and function represent a significant challenge to ecological planning and management (Hannah et al., 2007). Consequently, climate adaptation planning has become a central objective of ecological planners in recent years (Stein et al., 2013). Historically, ecological reserves have been viewed and managed as static entities (Bengtsson et al., 2003; Ndubisi, 2002). However, changing climate conditions will alter the boundary conditions of ecosystems at the most fundamental level. Given these projected future changes, maintaining stasis in ecosystems, even within a bounded range of variability, will not be feasible (Stein et al., 2013). Instead, ecosystem management will need to accommodate change, in many cases to the point of system transformation (Millar et al., 2007; Stein et al., 2013). Understanding the spatial response of individual species and ecological communities to climate change is central to this effort (Hannah et al., 2002; Hole et al., 2011).

Despite the uncertainties involved with projecting how species and communities will respond to climate change, ecological plans must address these changes if they are to be effective (Hannah et al., 2002). The first logical approach is to reduce uncertainty by improving our understanding of how ecosystems and species will respond to future changes. There is a diverse array of information sources that can potentially provide this insight including climate and ecological response models, trait-based indices, and experimental and observational data (Dawson et al., 2011; Rowland et al., 2011). While each of these information sources contributes to our understanding of possible future climate impacts, they are each incomplete on their own. Consequently, integrating these resources into a coherent assessment of climate vulnerability or impact is essential. Despite the importance of drawing from a range of information sources, the majority of existing case studies of adaptation planning have largely relied on expert opinion and general characterization of climate impacts (Cross et al., 2012; Poiani et al., 2011). Much of this omission is likely due to the limited availability of information resources such as quantitative, ecological response model projections for most regions. As the availability of climate vulnerability information increases, managers need practical guidance for how to apply these resources to management decisions at the landscape scale.

Even when vulnerability and adaptation plans are able to incorporate a wide array of information sources, the complex nature of ecosystems and the scale of change expected means that significant uncertainty will undoubtedly remain (Millar et al., 2007). At a basic level, while a growing number of studies have used both statistical and process-based models to project changing species and vegetation distributions (e.g. Bachelet et al., 2001; Lawler et al., 2009; Rehfeldt et al., 2006), the accuracy of these projections remains highly uncertain due to assumptions inherent to each model, limited empirical data for model parameterization, and inherent uncertainty in climate change projections themselves (Angert et al., 2011; Beier and Brost, 2010; Davis et al., 1998; Gilman et al., 2010; Pearson and Dawson, 2003). Efforts to evaluate sensitivity to climate change based on inherent species and habitat characteristics are limited by a paucity of natural history data relative to the diversity of biological systems we seek to understand. Efforts to use natural history characteristics to predict which species will respond to climate change by shifting their geographic range have met with limited success (Angert et al., 2011). Finally, modifying plant and animal community composition through climate-induced range shifts will have cascading but highly uncertain impacts on community interactions and ecosystem function (Gilman et al., 2010).

Fundamentally, the complexity of ecological systems poses significant challenges to predicting future ecological conditions (Levin, 1998). This is especially true given the far reaching, pervasive and intense projected impacts from climate change (Grimm et al., 2013). Future uncertainty is a significant but not insurmountable barrier to developing ecological climate adaptation plans (Millar et al., 2007; Stein et al., 2013). Scenario planning is one potentially promising approach to incorporating uncertainty into the planning process (Gillson et al., 2013; Peterson et al., 2003; Stein et al., 2013). While adaptation planning routinely incorporates climate scenarios (Cross et al., 2012; Snover et al., 2007), uncertainty as to how ecological systems will respond to climate change is substantial and projections of response vary widely even within the same climate scenario. The role of scenarios in adaptation planning needs to be expanded significantly to help address uncertainty and facilitate creative and flexible management approaches. In particular, scenarios need to expand to include uncertainty as to how ecosystems will respond to climate changes explicitly.

Research Objectives

Incorporating human-dominated landscapes and climate change into ecological planning and management are the two most significant challenges for ecological planning over the next century. Many significant impacts of these drivers will be mediated by the interactions between landscape structure, biodiversity and ecosystem function. In my dissertation, I explore these interactions from two different perspectives. First, I empirically measure how landscape and habitat patterns influence *Q. garryana* stand structure across an urban gradient (Chapter 1) and whether and how early regeneration processes differ between urban and non-urban oak stands (Chapter 2). My central hypothesis is that urban development at the landscape scale alters the presence, absence, and abundance of animal species that interact with *Q. garryana*. In this way, urban development alters the context within which oak regeneration takes place. At finer scales, the type and spatial arraignment of habitat as well as interactions among foraging individuals alter foraging, competition, and caching behavior. In addition, I expect that seedling and sapling abundance will differ in urban environments due to either altered dispersal processes or altered environmental conditions or both, leading to differences in acorn germination, seedling production and survival. Overall, I hypothesize that urbanization alters environmental, or coarse-scale, constraints on oak regeneration which combines with fine-scaled interactions among foraging seed-dispersers and local habitat conditions to generate unique seed dispersal and regeneration patterns in urban landscapes. I track the dispersal and fate of individual acorns directly to test whether dispersal processes differ in urban and non-urban landscapes and use experimental acorn plantings and observational comparisons of seedling and sapling abundance to test whether urban development influences later stages of oak regeneration.

In Chapter 3, I seek to contribute to our ability to evaluate climate vulnerability and develop adaptation strategies for ecological systems at the landscape scale despite significant uncertainty in how climate change will affect biodiversity, community composition, and ecological processes. I review the range of information resources available to ecological planners for conducting ecological climate change vulnerability assessments and present a checklist of questions to help ecological planners identify consensus, disagreement, and knowledge gaps in projections of future resource condition. Finally, I propose that planners can use the vulnerability assessment to develop "resource response" scenarios, or scenarios of how a priority species or system will respond to climate change, to facilitate the development of robust climate adaptation strategies. Scenario planning has been suggested as a potentially useful approach for planning when the future is highly uncertain (Peterson et al., 2003). While conducting formal scenario planning is a resource intensive process (Baker et al., 2004; Peterson et al., 2003), creating even simple scenarios can help managers consider a wide range of actions and identify those that may be robust to a range of future conditions. I use the management of *Q. garryana* in the Willamette Valley, OR as a case study to illustrate how planners can integrate information drawn from diverse information resources and develop simple scenarios to help identify and evaluate management actions to facilitate climate adaptation for this species.

CHAPTER 1

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

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 led 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 (Acácio et al., 2010; Fischer and Bliss, 2008; Hougner et al., 2006). As a result, Oregon white oaks are the subject of significant restoration and protection efforts throughout their range (Fuchs, 2001; Larsen and Morgan, 1998; MacDougall, 2008). In Pierce and Thurston counties, WA, 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 animal dispersers provide two important services that both increase germination and survival: they carry acorns away from the parent tree reducing density dependent mortality (Howe and Miriti, 2000; Janzen, 1970), and they bury, or cache, acorns reducing the risk of desiccation (Fuchs et al., 2000). In the study region, western gray squirrels are not known to occupy forest patches in urban areas (Ryan and Carey, 1995), while 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., 2004b), 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., 2004a), 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 Ramon Obeso, 2003; Herrera and Garcia, 2010; McEuen and Curran, 2004). 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 (1999) 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, and so 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., 1999; Kollmann and Buschor, 2003; Pérez-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 this study area, 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, for example 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.

METHODS

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 1.1). Oregon white oaks often form relatively distinct stands (referred to here as oak woodlands), which are distributed throughout this 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, WA, but averages only four cm per month during the growing season between April and September (WRCC 2010). JBLM is over 35,000 hectares 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.

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 hectares. 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 hectares. Oak woodlands less than one hectare 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 meters above sea level and all woodlands are 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 half kilometer of each oak woodland site. I chose this distance because field research has indicated that it captures the approximate 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 meter 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 ten-meter radius plots nested within each of the 30 oak woodland sites. Plot center locations were randomly generated using HawthsTools 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 > 2m tall and < 10 cm DBH. I counted oak seedlings (< 0.5 meters tall) in four one-meter radius subplots. The center of each subplot was located five meters in each cardinal direction (N, S, E, and W) of the ten-meter radius plot center.

Canopy and understory composition were visually estimated for the ten-meter plot and each of the one-meter seedling subplots. Both canopy and understory were analyzed separately as continuous (Table 1.1) and categorical variables. To create canopy categories, I binned the one-meter 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 1.1).

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 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 $\alpha \leq 0.05$.

RESULTS

A total of 128 ten-meter plots and 554 one-meter plots were included in the final analysis, after removing all plots and subplots with un-natural (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 1.1). Using canopy composition as a categorical variable showed that oak seedlings were least abundant under non-forest canopy (Figure 1.2). Comparing seedling abundance under closed, mixed and open canopy conditions again showed that abundance is lowest in open conditions (Figure 1.3). Oak seedling abundance appeared to peak under mixed canopy closure conditions, but this was 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 1.1), and least abundant in plots with open forest canopy (Figure 1.4). Young (class 1) saplings showed no relationship to canopy cover (Table 1.1, Figure 1.5).

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 1.1). 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. Seedling abundance was strongly positively correlated with grass understory (Table 1.1), and seedlings were most abundant in grass-dominated and mixed subplots (Figure 1.6). 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 1.1). In addition, both classes were most abundant in plots dominated by shrub cover (Figure 1.7, Figure 1.8). 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 1.1).

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 1.1, *p-value* = 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 1.9).

DISCUSSION

Effects of Canopy Cover

Recruitment patterns within oak stands appear to change overtime. Oak seedlings were most abundant under oak canopy (Table 1.1, Figure 1.2), but older (class 2) saplings were less abundant with increasing adult oak basal area and DBH (Table 1.1). 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 Davis, 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 1.2). 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., 1999; Gómez, 2003; Gómez et al., 2008; Pons and Pausas, 2007). The second explanation is not supported by a study by Fuchs et al. (2000), 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 1.6), 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 (Kollmann and Buschor, 2003; Munoz and Bonal, 2007; Pérez-Ramos and Marañón, 2008; Smit et al., 2001), and is generally reduced in open habitats (Hulme, 1998). Fuchs and others (Fuchs et al., 1999) 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 (Figure 1.7, Figure 1.8). 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 (2000) 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 1.9) 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 (Bender et al., 2004; Etter et al., 2002). High deer densities can cause significant damage to vegetation through overgrazing (Côté et al., 2004; Horsley et al., 2003; Stromayer and Warren, 1997). In addition to deer, eastern cottontail rabbits (*Sylvilagus floridanus*) spread rapidly throughout western

Washington after their introduction in 1927 (Dalquest, 1941). While 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 Litvaitis, 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 as well. 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., 2000; Johnson et al., 2009). 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 un-mowed 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 were not 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. Conversation 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 1.1). 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 1.2) 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 1.9), and older sapling abundance is not significantly different (Table 1.1). 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 (Callaway, 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 (Gómez-Aparicio et al., 2008; Herrera and Garcia, 2010; Robinson and Handel, 2000). 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 (Gómez-Aparicio et al., 2008). Planting oak seedlings or targeting management of naturally occurring seedlings in shrub cover could improve restoration success and reduce maintenance costs.

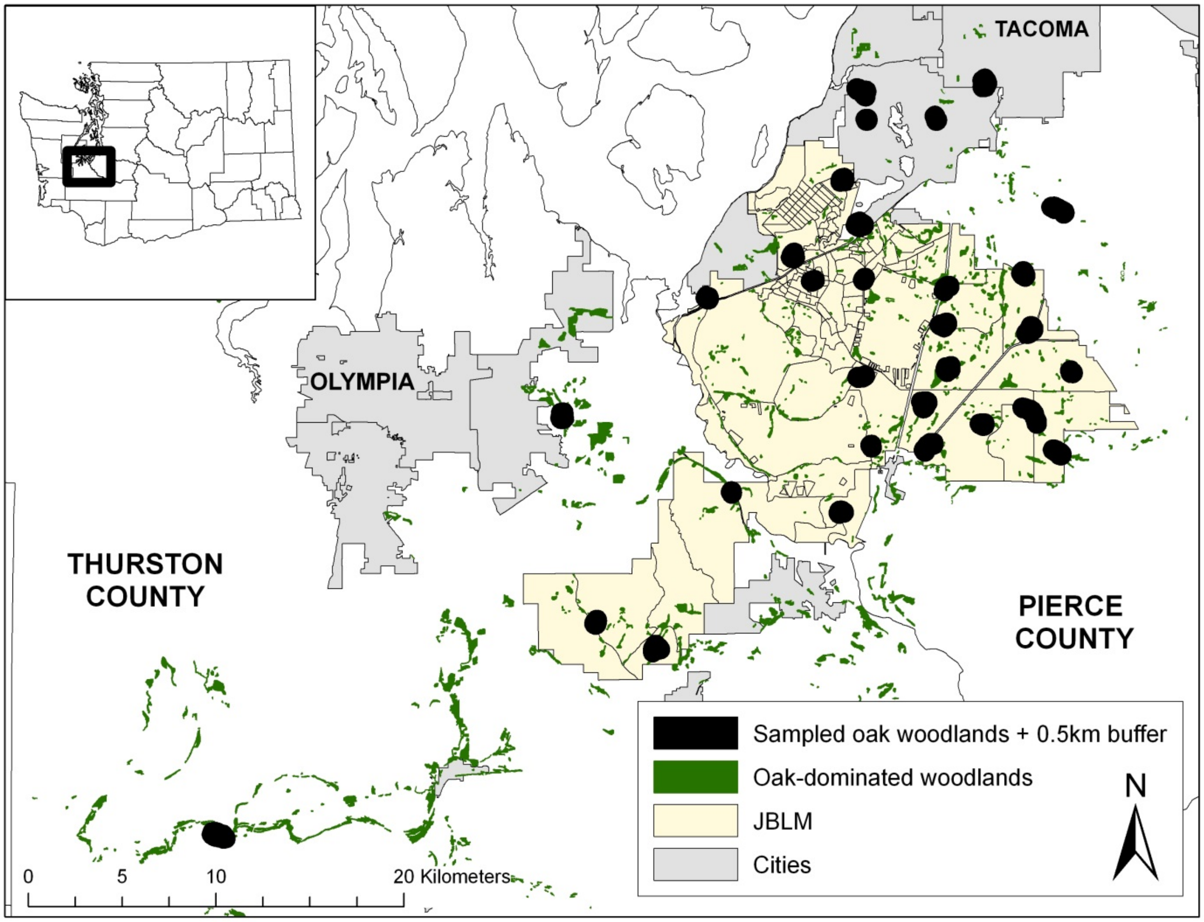

Figure 1.1. Map of study area.

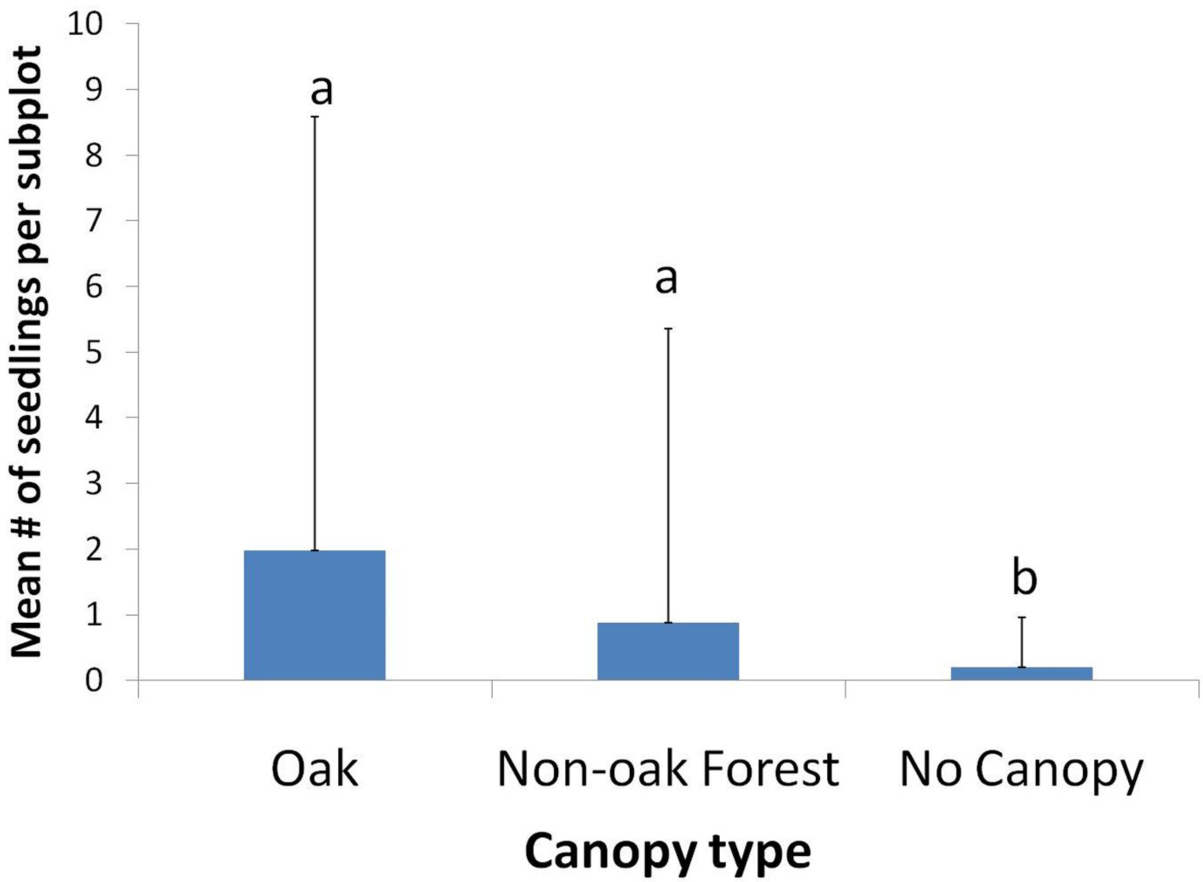

Figure 1.2. Mean number of seedlings (+1 sd) by canopy type. Oak = some oak canopy present (oak canopy > 0%), non-oak forest canopy = some forest present, but no oak canopy present (oak = 0% and conifer + deciduous + shrub > 0%), and open = no forest canopy cover (open = 100%). Categories labeled with the same letter are not significantly different (*p-value* > 0.05).

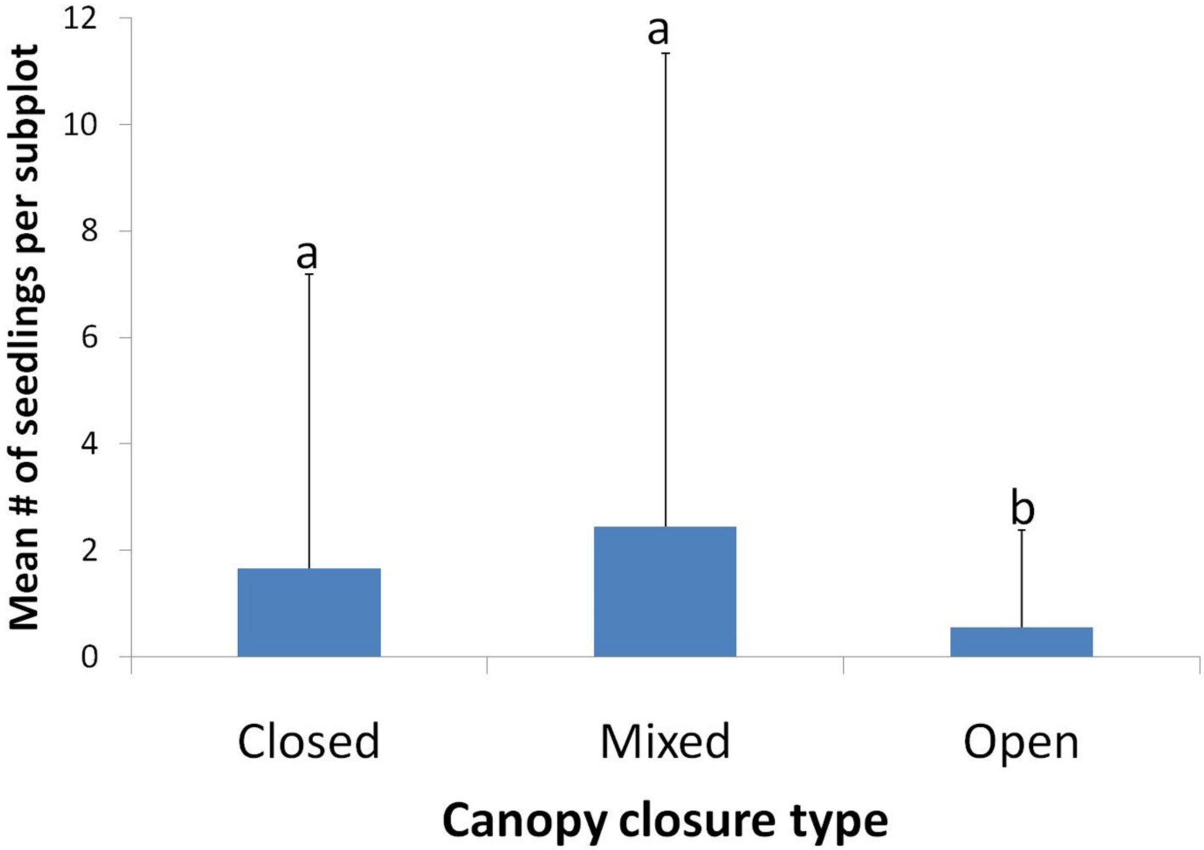

Figure 1.3. Mean number of seedlings (+1 sd) by canopy closure type: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). Categories labeled with the same letter are not significantly different (*p-value* > 0.05).

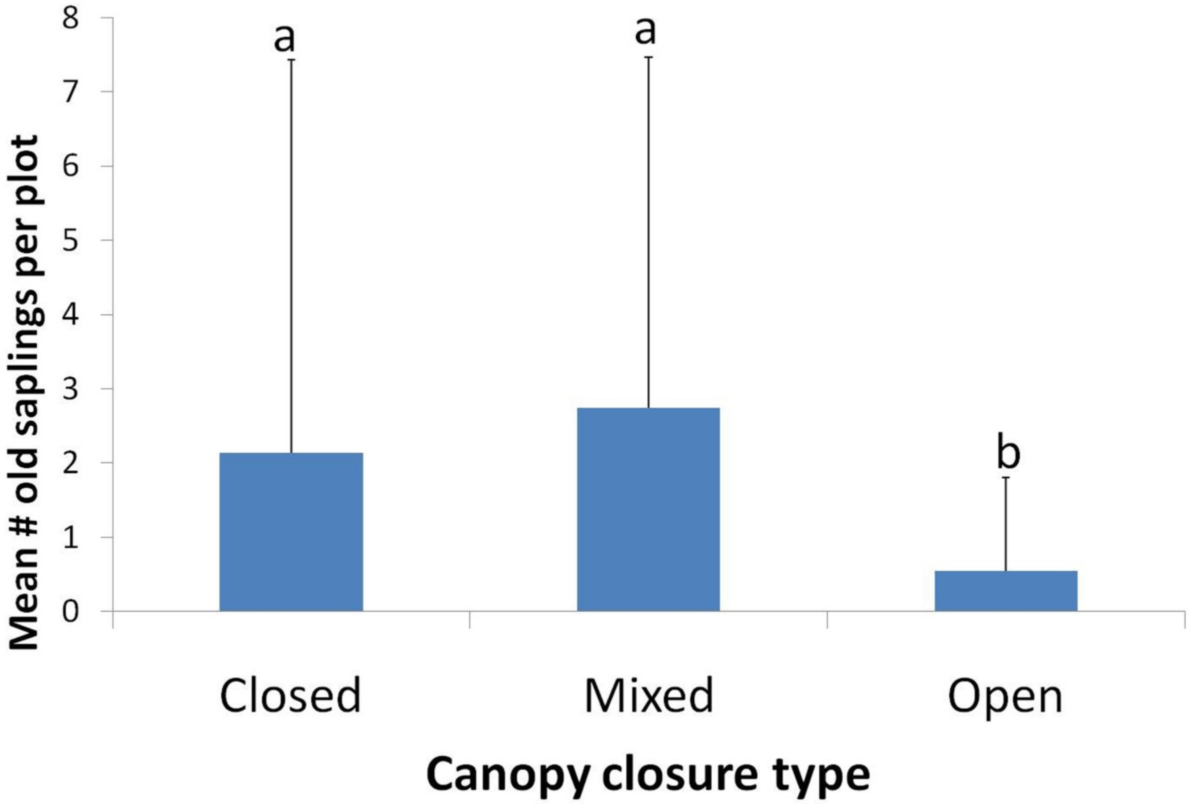

Figure 1.4. Mean number of old (class 2) saplings (+1 sd) by canopy closure type: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). Categories labeled with the same letter are not significant (*p-value* > 0.05).

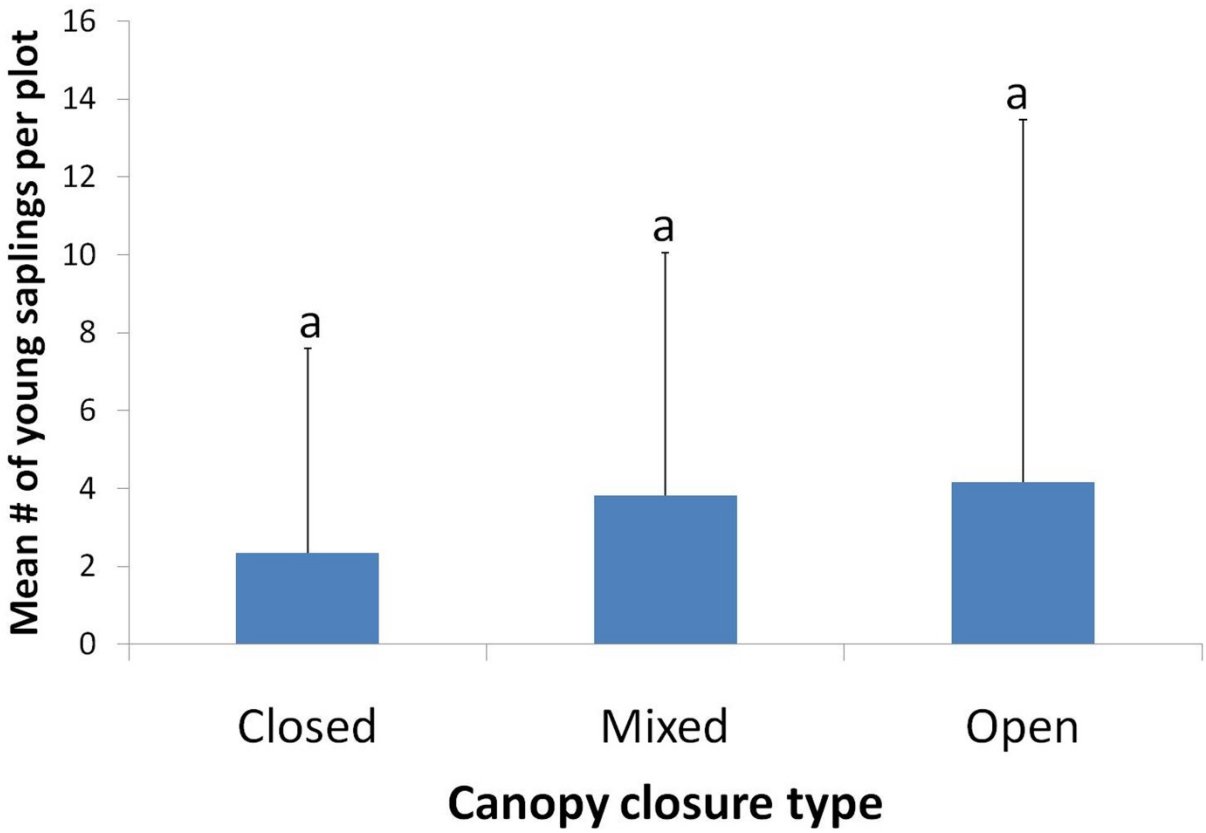

Figure 1.5. Mean number of young (class 1) saplings (+1 sd) by canopy closure type: sparse canopy (≤ 30% forest canopy), mixed canopy (> 30% and ≤ 60% forest canopy) and dense canopy (> 60% forest canopy). Categories labeled with the same letter are not significantly different (*p-value* > 0.05).

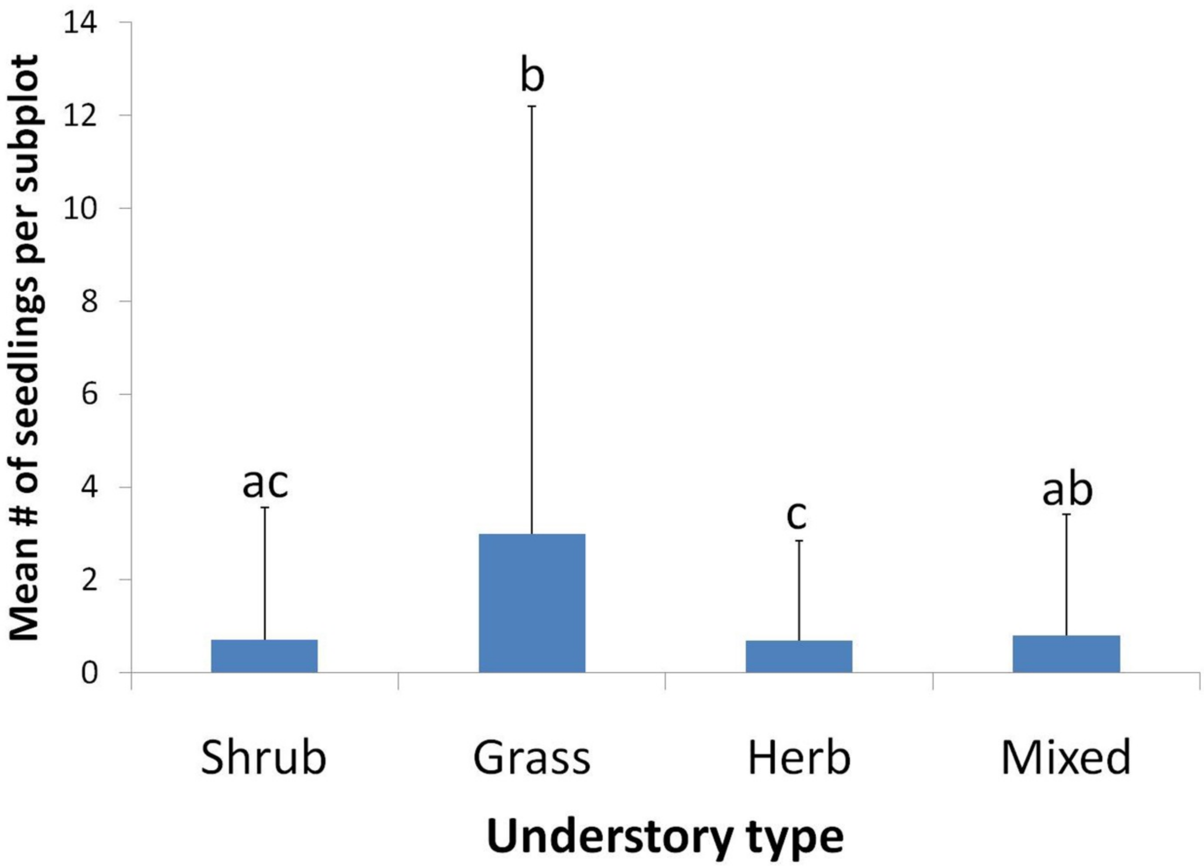

Figure 1.6. Mean number of seedlings (+1 sd) by dominant understory category. Categories labeled with the same letter are not significantly different (*p-value* > 0.05).

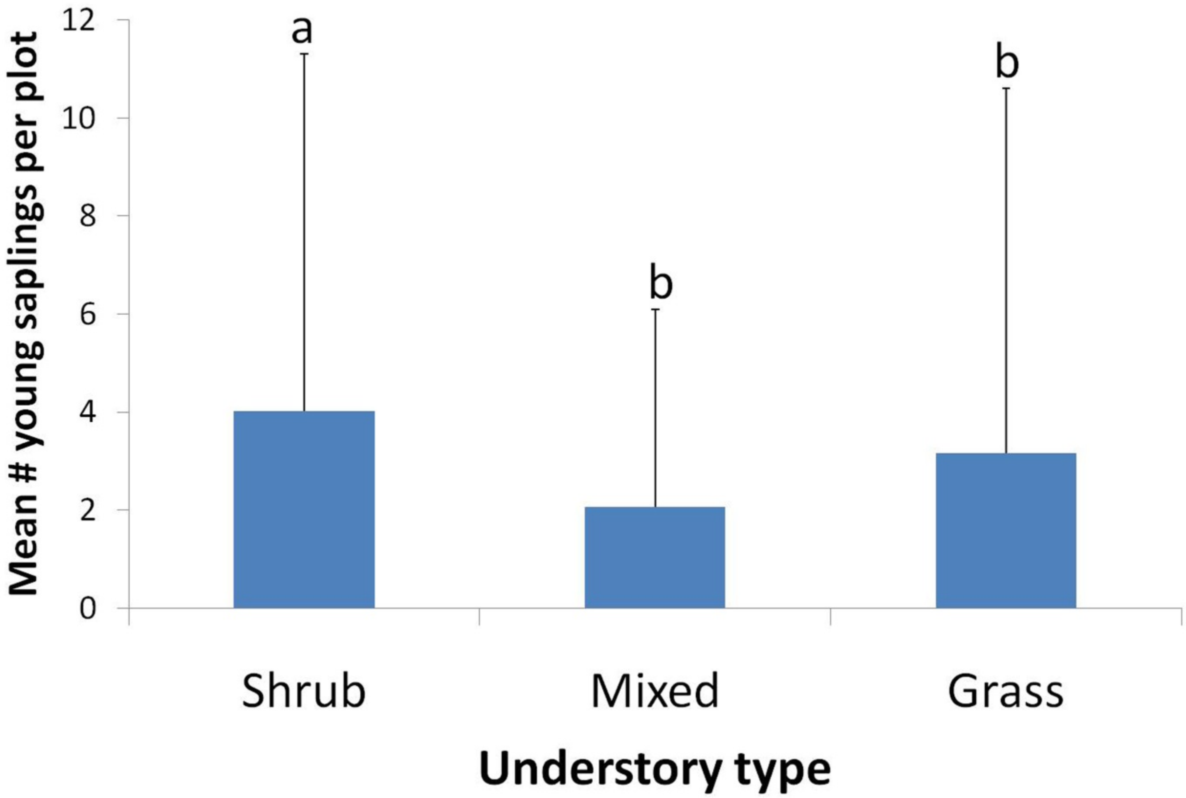

Figure 1.7. Mean number of young (class 1) saplings (+1 sd) by dominant understory category. Categories labeled with the same letter are not significantly different (*p-value* > 0.05).

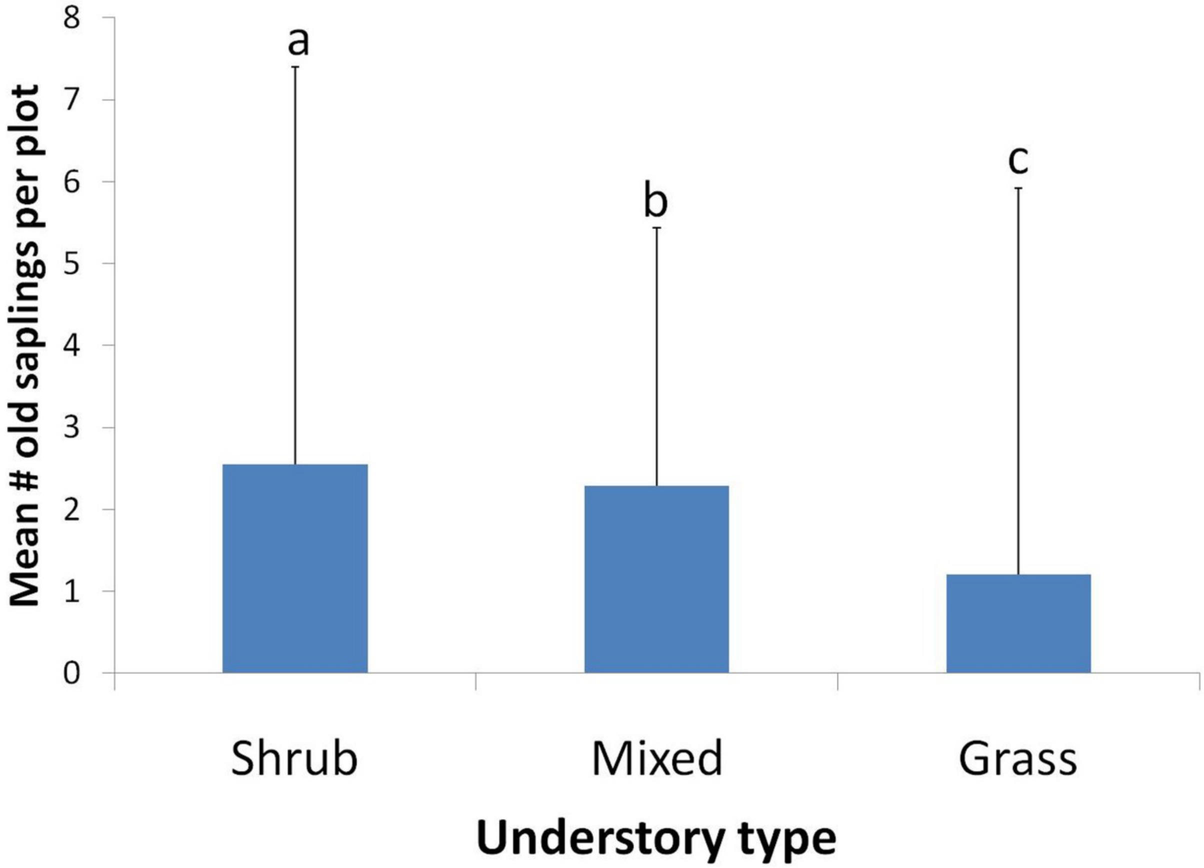

Figure 1.8. Mean number of old (class 2) saplings (+1 sd) by dominant understory category. Categories labeled with the same letter are not significantly different (*p-value* > 0.05).

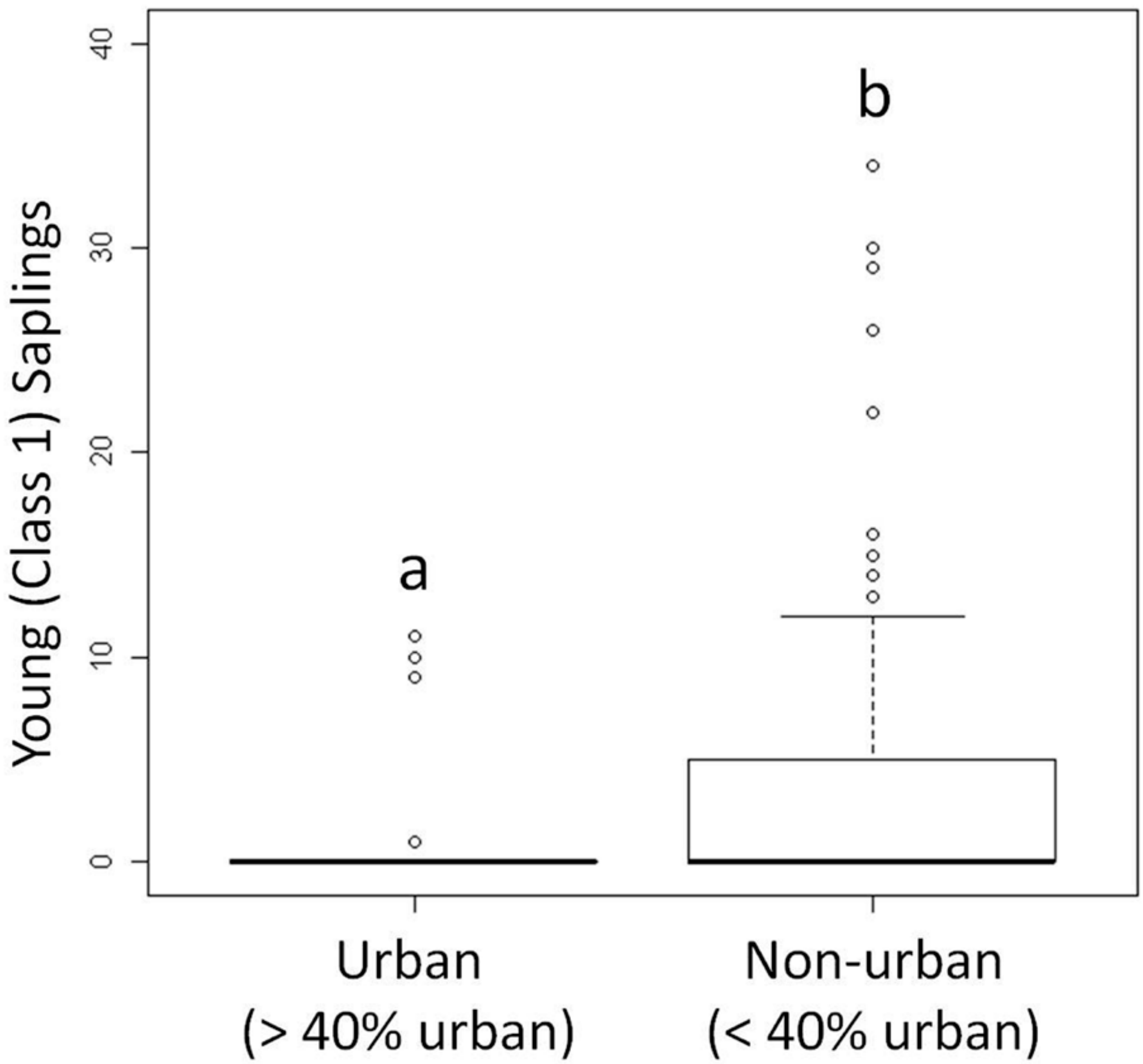

Figure 1.9. Comparison of young (class 1) sapling abundance in urban and non-urban oak woodlands. Categories labeled with different letters are significantly different (*p-value* = 0.05).

Table 1.1. 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 $\alpha < 0.05$. 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

CHAPTER 2

Effects of Urban Development and Landscape Structure on Oregon White Oak (*Quercus garryana*) Dispersal and Early Regeneration Patterns and Processes

INTRODUCTION

Numerous studies have documented altered plant and animal community composition in remnant habitat fragments that are surrounded by urban development (Faeth et al., 2011; McKinney, 2006). Changes to animal community composition can have significant implications for animal-mediated ecosystem services such as pollination (Kremen et al., 2002) and seed dispersal (Markl et al., 2012). Seed dispersal is a critical ecosystem process that sustains biodiversity in forest ecosystems (Howe and Miriti, 2000; Janzen, 1970; Levin et al., 2003; Markl et al., 2012). Anthropogenic changes to landscape structure can alter seed dispersal patterns at multiple scales (Markl et al., 2012; McConkey et al., 2012) with significant implications for forest regeneration and diversity (Chapman et al., 2003; Cordeiro and Howe, 2003).

In rural landscapes, forest fragmentation can alter seed dispersal patterns by changing the presence, absence, and abundance of seed-dispersing animals (Gardner et al., 2009; Moran et al., 2004). In addition, within landscapes, the amount and spatial arrangement of habitat features such as forest cover can strongly influence animal movements and subsequent patterns of dispersal and regeneration (Alcántara et al., 2000; Gómez, 2003). While these relationships are well established in agricultural landscapes (Breitbach et al., 2010; Chapman et al., 2003; Cordeiro and Howe, 2003; Santos et al., 1999), similar studies have not been conducted in urban landscapes. Improving our empirical knowledge of how changes to landscape structure and biodiversity influence ecosystem function in urban landscapes is critical for understanding and managing urban ecosystems.

Oregon white oak (*Quercus garryana* Douglas ex Hook.) provides an ideal case study for investigating the impacts of urban development on animal-mediated seed dispersal. *Q. garryana* is the only native oak in Washington State and is a species of conservation concern throughout its range (Larsen and Morgan, 1998). In the Pacific Northwest, much of this species' current habitat is located in the rapidly urbanizing Puget Sound-Willamette Trough. Within this region, numerous oak woodlands are currently protected in city parks in and around the cities of Olympia and Tacoma, WA and Portland, OR, and continuing urban expansion could lead to more oak stands being embedded in urban landscapes. Local governments and conservation groups have expended significant effort to protect *Q. garryana* woodlands in both urban and rural areas (Larsen and Morgan, 1998). However, these efforts focus solely on adult trees with little knowledge of whether regeneration within protected urban stands is sufficient to sustain the population.

Q. garryana acorns rely on a comparatively small number of animal species for dispersal (Larsen and Morgan, 1998) and urban development is known to influence the distribution and abundance of these species (Ryan and Carey, 1995; Vigallon and Marzluff, 2005). Acorn-dispersing species include native Steller's jays (*Cyanocitta stelleri*), native western gray squirrels (*Sciurus griseus*), and non-native eastern gray squirrels (*Sciurus carolinensis*). Western gray squirrels are not known to occupy forest patches in urban areas (Ryan and Carey 1995) while 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). Dispersal services provided by animals are theoretically important for *Q. garryana* because oaks are considered dispersal limited due to their large seed size (Fuchs et al., 1999; Larsen and Morgan, 1998). Dispersal by squirrels and jays can benefit *Q. garryana,* because acorns are carried away from the parent tree, facilitating the spread of the species, and buried, or cached, which reduces predation and increases germination (Fuchs et al., 2000).

Dispersal quality can be quantified and compared by measuring the following individual stages of the dispersal process: acorn removal or "handling," predation, germination, dispersal distance and seedling production. Alterations to landscape structure and the composition of the acorn-dispersing animal community can potentially influence each of these stages. Seeds that are picked up, moved, dispersed, and/or eaten by seed-dispersing animals are all considered "handled." In an experimental context, seeds are considered "handled" if they have been removed from the experimental plot or feeding station. Handling can be considered a measure of foraging activity and higher handling rates are beneficial if removed seeds are dispersed to new locations intact (Carlo and Morales, 2008). Several studies have found higher seed removal from experimental feeding patches in urban compared to non-urban environments. Shochat et al. (2004a) found that foraging birds consistently removed more seeds from experimental patches in urban Phoenix compared to outlying desert areas. Bowers and Breland (1996) found that squirrels foraging near human habitation also removed more seeds from experimental patches than squirrels in rural areas. However, neither of these studies evaluated seed dispersal after removal.

Acorn predation measures the proportion of handled acorns that are consumed. Many studies use seed removal as a proxy for predation (Fuchs et al., 2000; Kollmann and Buschor, 2003; Smit et al., 2001). However, in the case of oak acorns, once an acorn is handled, it may be eaten or cached intact. The rate of acorn consumption determines whether a seed disperser's contribution to oak reproduction is positive or negative (Hulme, 1998). Therefore, assuming that all handled acorns are eaten is not only flawed, but also missing the most important measure of dispersal effectiveness, which is the number of acorns that are dispersed, cached and left intact to germinate (Vander Wall et al., 2005). Because most studies do not measure predation directly, little is known about what factors influence seed predation rates. Munoz and Bonal (2007) found that seed predation rates can increase in more competitive environments. In urban landscapes, higher competition may lead to higher predation rates on dispersed seeds if food resources are limited as squirrels and jays would need to rely more heavily on cached stores during winter. In addition, different acorn-dispersing species may exhibit differing rates of predation (Schupp et al., 2010). Lastly, higher productivity and greater food resource availability in urban environments (Faeth et al., 2005) may decrease squirrel and jay reliance on cached acorns and therefore reduce predation rates.

Acorn dispersal is measured as the distance an acorn travels after it has been removed from the parent. Gray squirrels are scatter-hoarders, meaning that they store individual acorns in separate, dispersed locations as opposed to larders. Longer distances between caches reduce the chance of pilfering, but also increase the amount of energy expended to cache and retrieve seeds. Consequently, when the risk of pilfering is high, such as when food resources are scarce, dispersal distances should be longer (Moore et al., 2007). In addition, Hopewell et al. (2008) found that increased competition among eastern gray squirrels led to shorter dispersal distances as squirrels prioritized gathering more nuts, over hiding acorns more effectively, by taking them longer distances. Consequently, both a higher density of individuals and variation in resource abundance in urban versus non-urban areas could affect dispersal distances.

Finally, for animal dispersed seeds, the behavior and habitat preferences of animal dispersers interact with the spatial structure of the landscape to produce observed patterns of seed deposition (Russo et al., 2006). Specifically, the amount and spatial distribution of forest or shrub cover can also influence seed dispersal patterns (Alcántara et al., 2000; Fuchs et al., 1999; Gómez, 2003). Habitat use of both squirrel species is tightly linked to forest cover density (Johnston, 2013) and Steller's jays prefer to cache acorns under forest cover (Fuchs et al., 1999). In addition, *Q. garryana* seedlings are significantly more abundant under conifer forest compared to non-forested grassland sites, suggesting that forest cover may be an important factor driving patterns of acorn dispersal and regeneration (Michalak, 2011).

In this chapter, I analyze whether urban development at the landscape scale and forest cover patterns within landscapes influence seed dispersal processes and regeneration patterns in *Q. garryana* woodlands. I quantify spatial patterns of seed dispersal by tracking seed movements directly and assess regeneration by quantifying acorn germination and seedling production rates using experimental acorn planting plots. The specific goals of this study are to: 1) test whether dispersal services and subsequent regeneration processes differ in oak woodlands located in urban versus non-urban landscapes; 2) test whether habitat composition including forest and shrub cover patterns influence oak dispersal processes and forest regeneration; and 3) characterize the importance of dispersal services provided to *Q. garryana* acorn in the south Puget Sound.

METHODS

Study Area

The study area is located at the southern end of the Puget Sound Trough within the western third of Pierce County, WA (Figure 1.1). *Q. garryana* often form relatively distinct stands (referred to hereafter as oak woodlands), which are present in both the highly urbanized Tacoma metropolitan region and on the Joint Base Lewis-McChord (JBLM) military installation. JBLM is over 35,000 hectares 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 urbanization on *Q. garryana* dispersal and regeneration processes.

I identified five urban protected areas containing oak stands (referred to here as sites 12, 18, 67, 75, and 90) and four "non-urban" oak stands (sites 198, 252, 333, and 398) of similar size located in the undeveloped sections of JBLM. All study sites were located on public lands and contain between 1 and 10 hectares of oak stands. Selected urban oak stands were surrounded by more than 50% urban[1] land cover within a 1-kilometer radius of the oak stand boundary. Non-urban oak stands contained less than 30% urban land cover within a 1-kilometer radius. At these non-urban sites, areas of the landscape classified as urban land cover included paved and gravel roads and occasional small buildings associated with rifle ranges and ammunition storage. While the non-urban stands lacked urban infrastructure, they did experience intense human use during military training periods. Outside of military training, these areas were rarely used. Elevation of the study area ranges from 10 to 200 meters above sea level 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).

Eastern gray squirrels were observed in all urban oak woodland sites. Western gray squirrels are not known to occupy urban areas (Johnston, 2013; Ryan and Carey, 1995), and hair-snag traps set near acorn plots failed to detect western gray squirrels in these sites. The

[1] Refers to heavy (> 80% impervious per 30-m pixel), medium (50-80% impervious per pixel) and light (20-50% impervious per pixel) landcover (Alberti et al., 2006).

Washington Department of Fish and Wildlife and the Department of Defense provided detailed data on the presence/absence of eastern and western gray squirrels on JBLM (Johnston, 2013). These data revealed that western gray squirrels were present and active at sites 252, 333, and 398. Eastern gray squirrels had been experimentally removed from sites 252 and 398 and remained undetected at these sites throughout my study. Finally, both squirrel species rarely used site 189 (Johnston, written communication).

Acorn Production

Q. garryana acorn production is highly variable from year to year and a number of tree, site and environmental factors have been shown to influence acorn production on individual trees in this study area (Peter and Harrington, 2002). To gauge yearly variation in acorn production at my field sites, I selected 15 trees (8 urban and 7 non-urban) with high production potential to monitor all three years of the study (2009, 2010, and 2011). I defined trees as having high production potential if they were: 1) in healthy condition; 2) greater than 1.3 meters tall with a diameter of 20 cm or more at breast height; 3) had a maximum of 50% of their crown perimeter in contact with other trees; 4) formed either a columnar or mushroom shape crown. Research has shown that *Q. garryana* trees with these characteristics are more likely to produce large acorn crops (Peter and Harrington, 2002). I evaluated acorn production on a scale of 1 to 4, with 1 being non-producing, 2 being light producing (acorns not readily visible, but present), 3 being moderate producing (readily visible but patchy) and 4 being heavily producing (acorns covering the tree) following the methods outlined in Peter and Harrington (2002).

Acorn Collection

I collected acorns during the second half of September in 2009, 2010, and 2011 from the study sites and surrounding areas. All acorns were brought into the lab from the field and soaked in water to remove dirt and insects and fully hydrate the acorns. Acorns that floated (indicating that they were not sound) or that had obvious disease or insect damage were discarded (Fuchs et al., 2000; Gómez et al., 2008). Acorns were stored in a cool dark location in loosely closed plastic bags to retain moisture until planting (Fuchs et al., 2000).

Experimental Acorn Plots

During the last week of September all three years, I planted acorns in experimental plots in one of five micro-habitat types: oak canopy/grass understory, oak canopy/shrub understory, conifer forest canopy/shrub understory, conifer forest canopy/sparse herb understory, and grassland. I measured the presence/absence of canopy cover above each acorn location using a Cajanus tube resulting in a total of 30 canopy cover point measurements per plot. Canopy cover per plot was then estimated as the mean of these measurements (Korhonen et al., 2006). A minimum of 66% of canopy cover for the plots defined as "oak" was comprised of oak. The canopy of conifer forest was predominantly (> 66%) Douglas-fir (*Pseudotsuga menziesii*) with a small percentage of madrone trees (*Arbutus menziesii*). Non-forest grassland sites had no forest canopy overhead. Shrub understory sites were dominated by snowberry (*Symphoricarpos albus*) and Indian plum (*Oemleria cerasiformis*). Sparse herb sites were dominated by moss and sparse sword fern (*Polystichum munitum*) with little to no shrub cover. These canopy and understory types were selected because they were significantly correlated with oak seedling abundance in previous vegetation surveys, and potentially influence the behavior of seed dispersal species

(Michalak, 2011). Eastern gray squirrels are more often found in habitats with shrub cover, while western gray squirrels prefer habitats with open herb understory (Johnston, 2013).

Plots consisted of three parallel rows, 0.5 meters apart, with 10 acorns per row each spaced 0.5 meters apart (Fuchs et al., 2000). I marked plot rows using a length of twine strung no higher than 10 cm off the ground between two stakes with a knot indicating the location of each acorn. Within each plot, acorns were randomly assigned to one of three treatments: planted just beneath the soil surface (hereafter referred to as planted), placed on the soil surface (surface)[2], and marked with a fluorescent flag and placed on the soil surface (tagged). Each tagged acorn had a small (1/16th inch) hole drilled through the cotyledon and 10 cm of 24 gauge wire inserted through the hole (Gómez et al., 2008). Five centimeters of orange flagging were attached to the wires and marked with a unique identifying number. Attaching flags to the acorns allowed for the recovery of acorns after they were removed from the plot. Tracking tagged acorns permitted me to determine additional information about acorn fate such as how far removed acorns were dispersed, whether removed acorns were consumed, and whether dispersed acorns ultimately germinated and produced seedlings. Tagging does not significantly affect dispersal behavior (Xiao et al., 2006).

I placed acorns in their plots during the last week of September during the natural dispersal period in 2009, 2010 and 2011. The 2009 field season was used as a pilot study to test field methods. During this year, I distributed acorns across 31 plots in two sites, one urban and one non-urban. However, because 2009 was a high acorn production year, data collected during this pilot study provide an insightful contrast to the full study results obtained in 2010 and 2011. Therefore, these 2009 data are summarized in the results, although the sample size was smaller. In 2010 and 2011, I distributed acorns across a total of 54 plots (per year) in 5 urban and 4 non-

[2] Surface acorn treat was applied in 2010 and 2011 only.

urban sites (see Supplementary Table 1). In total, I distributed and observed 1391 tagged acorns, 1389 planted acorns, and 1080 un-tagged surface acorns for a total of 3860 acorns across all years and treatments. Plots were checked for dispersal, predation and germination every other week for three weeks starting the first week in October 2009, 2010, and 2011. Plots were re-visited the first week of June in 2010, 2011 and 2012 to evaluate seedling production and spring fate. I monitored survival of seedlings produced in 2010 for all three years and seedlings produced in 2011 for two years.

For un-tagged acorns, I recorded whether the acorn was handled, whether the acorn had germinated, and final fall and spring fates. Detailed descriptions of acorn fate categories are provided in (Table 2.1). For tagged acorns, I also recorded the distance the acorn was moved from its original location (if it was moved), the direction the acorn moved, and whether the acorn was buried. In 2010 and 2011, I also recorded the dominant understory type (grass, shrub, open/herb) of the new location within a 0.5-meter radius of the acorn, and the dominant canopy type (oak, conifer, shrub, or grassland) directly above the acorn's new location. I considered a tagged acorn "handled" if it was moved more than 10 centimeters from its previous marked location. This is because if an un-tagged acorn moved more than 10 centimeters, it would not be relocated and therefore would be counted as handled. I used two distance thresholds to define whether an acorn would be considered "dispersed:" 50 cm (Gómez et al., 2008) and 5 meters. The five-meter threshold is equivalent to the mean canopy radius (from the tree trunk) based on field measurements of 95 adult *Q. garryana* trees (Michalak, unpublished data). Essentially, five meters is a conservative estimate of the distance that an acorn would need to move to escape the parent oak canopy. For all recovered, tagged acorns, I was also able to definitively determine whether the acorn was depredated or not.

To recover tagged acorns, I searched for a minimum of 20 minutes and within 100 meters of the plot or until I had located all tagged acorns. I recorded the location of acorns dispersed more than 5 meters using a Trimble GPS. I marked the exact location of moved acorns in the field with flagging above the location if possible, and always by placing a small stick, protruding no more than 1 cm from the ground, adjacent to the new location. This allowed me to determine whether acorns had moved multiple times, without providing an obvious visual cue to seed predators. I measured all distances from the original acorn location within the plot and used the longest recorded distance for distance analysis.

Seedling Transects

I counted oak seedlings and saplings along transects that extended perpendicularly from the edge of oak woodlands into either conifer forest or into non-forested grasslands. I also surveyed transects extending across non-forested grasslands into conifer forest cover (gap transects) in both urban and non-urban landscapes. Transects began at the base of an adult oak tree (> 10 cm Diameter at Breast Height - DBH) and extended up to a minimum of 60 meters from this point. I extended transects beyond 60 meters as long as I continued to find seedlings within the next 10 meters or until I encountered a second adult oak tree. I counted all seedlings and saplings located within two meters of the transect line, recorded the distance along the transect, and recorded the locations of the seedlings/saplings using a Trimble GPS. Transect locations were selected to avoid passing other adult oaks as much as possible in an effort to capture more data on seedlings at long distances from adult oaks (i.e. the tail of the dispersal curve). However, additional oaks were occasionally encountered along forested transects (i.e. within 60 meters of the transect). In these cases, I also measured the distance from transect seedlings/saplings to this nearest adult, recorded the DBH of the nearest adult and recorded the location of the adult with a GPS. Distance to additional nearest adults was measured using a tape measure for adults within 10 meters, a digital range finder for adults between 10 and 30 meters, and using GPS points and distance analysis with a GIS for adults more than 30 meters from the transect seedlings/saplings. Seedlings/saplings were then grouped into 10 meter interval distance bins based on the distance to the nearest adult for analysis.

Statistical Analysis

I used general linear mixed models to test for relationships between dispersal processes and landscape, plot, and treatment covariates. In all models, plots and sites were included as random variables. Acorns were nested within plots and plots were nested within sites. To test whether acorn dispersal processes differed significantly depending on landscape type (urban/non-urban), canopy cover type (oak, conifer, non-forest), understory type (grassland, shrub, sparse-herb), plot type (oak/grassland, oak/shrub, conifer/shrub, conifer/sparse herb, non-forest/grassland), field season year (2009, 2010, and 2011), and treatment (planted, surface, and tagged), I used general linear mixed models with a binomial distribution (lme4 package, R 2.13.0 software). Binary dispersal processes tested include: 1) whether the acorn was handled in the fall, 2) fall acorn germination of remaining (not handled) acorns, 3) fall acorn dispersal (i.e. whether an acorn was moved more than 50 cm or 5 meters), 4) fall acorn predation of tagged acorns that were both handled and recovered, and 5) spring seedling production of remaining acorns (see Table 2.1). I used general linear mixed models with a Gaussian distribution (lme4 package, R 2.13.0 software) to test whether dispersal distance of dispersed acorns (i.e. those that moved further than the two distance thresholds) differed depending on the plot and site characteristics listed above. I used the log-transformed, maximum distance recorded for each dispersed acorn. I tested for significance using the Likelihood Ratio Test and conducted pairwise comparisons using Tukey's honest significant difference tests. Significance for all tests was set at $\alpha \leq 0.05$.

I used transect data to test whether seedling abundance declined with increasing distance from adult oak trees. I only used transect data collected within the first 60 meters of the transect for comparability. I compared seedling abundance of different distance classes within and between canopy cover (conifer forest versus non-forest grassland) and landscape (urban versus non-urban) types using general linear mixed models with a Poisson distribution (nlme package, R 2.13.0). Transects were nested within sites. Significance for all models was set at $\alpha \leq 0.05$ unless otherwise noted.

RESULTS

For five of the plots used in the study, canopy cover and understory conditions differed slightly from the defined canopy cover conditions for other plots in the study. I analyzed the data with and without these five plots and found no significant qualitative difference in model results. However, for consistency, all results, summaries, and statistics reported here, except for distance results, have these five plots excluded. The final sample included 29 plots in 2009, 52 plots in 2010, and 53 plots in 2011 for a total of 134 plots with 1341 tagged acorns, 1339 planted acorns, and 1050 un-tagged surface acorns for a total of 3730 acorns across all years and treatments (see Supplementary Table 1). I used data from all plots in the distance summaries to maximize the sample of dispersed acorns and because canopy-cover type had no significant effect on distance results.

Of the 3730 acorns included in the final analysis, 68% (n=2545) were handled (i.e. removed from plots) by seed dispersers/predators (hereafter referred to as "dispersers") and 4.6%

(n=170) are known to have produced seedlings (see Supplementary Table 2). Of the 1341 tagged acorns, 65% were handled (n=872), 31% (n=418) were consumed *in situ*, 34% (n=454) were dispersed farther than 50 cm, 5% (n=78) were buried, and 20% (n=262) were consumed after dispersal. Only < 1% (n=7) of tagged acorns produced seedlings, and none of these were from dispersed acorns (Figure 2.2).

Acorn Production

Acorn production was significantly higher in 2009 compared to 2010 and 2011 (Figure 2.3). Acorn production was not significantly different between urban and non-urban areas overall or in any individual year. The variable "Year" was used as a proxy for acorn production in all subsequent analyses.

Acorn Handling

Habitat type, year (i.e. ambient acorn production), landscape type (urban/non-urban), and acorn treatment (planted, surface, or tagged) all influenced acorn handling (Table 2.2). Acorn handling was higher in habitats that provided cover and very low in non-forested grasslands (Figure 2.4). In all years, acorn handling was significantly higher under conifer forest canopy. Canopy density was not correlated with handling after controlling for canopy type (Table 2.2). Handling was higher in shrub and open herb compared to grass understory plots. Acorn handling was highest in 2010, when acorn production was lowest, moderate in 2011, and lowest in 2009 when acorn production was highest (Figure 2.4).

Treatment had a significant effect on acorn handling (Table 2.2). A post-hoc Tukey HSD test showed that overall, planted acorns were significantly less likely to be handled compared to acorns placed on the soil surface ($\alpha < 0.05$). In 2009, when there were only two treatments, planted and tagged, tagged acorns, which were placed on the soil surface, were more likely to be handled than planted (Figure 2.4). However, in 2010 and 2011 when both tagged and un-tagged acorns were placed on the soil surface, the un-tagged, surface acorns were significantly more likely to be handled than tagged acorns (Figure 2.4). In other words, given a choice between tagged and un-tagged acorns, seed dispersers will choose the un-tagged acorns.

Overall, animal dispersers handled significantly more acorns in urban sites than they did in non-urban sites (Table 2.2). Within years and cover types, acorn handling was consistently higher in urban than in non-urban sites and was significantly higher in conifer and oak plots in 2010 and 2011 (Table 2.2, Figure 2.5). Removal was significantly higher in urban oak and urban conifer forest compared to non-urban equivalent habitat types, but not significantly different between urban and non-urban grasslands.

Acorn Predation

Predation could only be consistently determined for tagged acorns and so is measured only using the tagged acorns that were both handled and for which final fall fates were determined ($n = 561$). Overall, 98% of handled acorns were consumed. In 2010 and 2011 and all years pooled, acorns removed from plots in urban sites were more likely to be eaten (Figure 2.7, Table 2.2). The predation rate was higher in 2010 (the low production year) than in other years (Table 2.2, Tukey HSD, $\alpha < 0.05$). The likelihood that a handled acorn was consumed was not affected by canopy cover type (oak, conifer forest, or non-forest grassland) (Table 2.2).

Acorn Germination

Germination rates were compared among all remaining acorns (i.e. those that were not handled). Germination was significantly higher in 2009 than all other years (Table 2.2, Tukey HSD, $\alpha < 0.05$). There was no significant difference in germination rate between 2010 and 2011. Germination rates were significantly higher for acorns planted beneath the soil surface, moderate in un-tagged surface acorns, and lowest in tagged surface acorns (Table 2.2, Tukey HSD, $\alpha <$ 0.05). Germination was significantly higher under oak canopy, moderate under conifer forest and lowest in non-forested grassland (Table 2.2, Tukey HSD, $\alpha < 0.05$). Germination was not significantly different between urban and non-urban sites (Table 2.2).

Seedling Production

Of all the acorns used in the study, only 4.6% produced seedlings (see Supplementary Table 2). The seedling production rate of all acorns was inversely related to acorn handling (Table 2.2). This finding is not surprising because the vast majority of handled acorns were consumed. Significantly more seedlings were produced in 2009 compared to either 2010 or 2011 (Tukey HSD, $\alpha < 0.05$), even when only analyzing acorns that were not handled. Planted acorns were more likely to produce seedlings than surface or tagged acorns (Tukey HSD, $\alpha < 0.05$). After controlling for handling, seedling production did not differ by landscape or habitat type (Table 2.2).

Although few seedlings were produced, seeding survival rates were generally high. In 2009, 16% of all acorns produced seedlings, 62% of these survived to a second year, and 44% of the initial seedlings survived to a third year. In 2010, 2% of all acorns produced seedlings and 49% of these survived to a second year (Supplementary Table 2). There were no significant effects of covariates on seedling survival except in the third year when understory significantly correlated with seedling survival (Table 2.2). In this case, seedlings in shrub understory were more likely to survive compared to those in grasslands (Tukey HSD, $\alpha < 0.05$).

Dispersal and Caching Behavior

Of the 1341 tagged acorns distributed, 65% were handled (either removed or eaten) by animals. Of the urban tagged acorns, 71% were handled of which 35% were consumed *in situ* and 36% were dispersed more than 50 cm (Figure 2.12). Of the urban acorns that were dispersed more than 50 cm, 90% were consumed after dispersal. None of the remaining dispersed acorns germinated or produced seedlings. In non-urban landscapes, fewer acorns were handled (59% of tagged acorns), fewer were consumed *in situ* (27%), and fewer were dispersed (32%) more than 50 cm (Figure 2.13). Of the dispersed non-urban acorns, 76% were consumed after dispersal and only one acorn germinated but did not produce a seedling. Only 5% of all dispersed tagged acorns were buried (Figure 2.2). In the urban landscapes, 92% of buried acorns were consumed and, of the buried acorns that were not consumed, none germinated. Comparatively, in non-urban landscapes only 48% of buried acorns were consumed, and 3% germinated, although none produced seedlings.

Acorns that were moved, were taken very short distances (mean ± 1 SE = 5.8 ±0.6 meters, range = 0.5-98.1 meters, median = 2.3 meters, N = 277 recovered acorns with at least one distance measure recorded). Only 34%, (n=454) were dispersed beyond 50 cm (assuming that lost acorns were moved at least 50 cm) and only 5% (n=75) were dispersed beyond 5 meters. The distribution was strongly right-skewed (skewness = 4.53; kurtosis = 27.67) (Table 2.3). Kurtosis and skewness were slightly higher for urban compared to non-urban acorns. The distribution of urban dispersal distances has a slightly higher peak and a slightly shorter but fatter tail compared to the distribution of non-urban dispersal distances which had a slightly longer but thinner tail (Figure 2.15).

I was able to collect at least one distance measure for all but 3% and was able to determine a final fall fate for all but 5% of tagged acorns. Tagged acorns that were not recovered were assumed to have moved at least 50 cm, since it is extremely unlikely that tagged acorns would not be found within 50 cm of their original location. In 2009, I distributed 291 tagged acorns and I was able to determine fall fates for 92%. In this first year, the wire connecting the flag to the acorn snapped for 17 of the unrecovered acorns, the acorn was taken and the flag left in place. Use of stronger wire in 2010 and 2011 corrected this issue. In 2010 and 2011, I set out 520 and 530 tagged acorns and recovered 91% and 99% respectively. The number of lost acorns was not significantly different between urban and non-urban sites (LRT, X^2= 0.4612, *p-value* > 0.05). By spring, I lost an additional 108 (8%) acorns for a total recovery rate at the end of spring of 87% (Table 2.4). Recovery was more difficult in the spring as fallen leaves and other debris were likely to obscure flagged acorns even if they remained within the search radius.

Acorns were significantly more likely to be dispersed (i.e. moved more than 50 cm) from plots under conifer or oak canopy compared to open grassland plots and more likely to be dispersed in 2010 compared to 2009 or 2011 (Table 2.5, Figure 2.14). Slightly more acorns were dispersed more than 50 cm in urban compared to non-urban sites, but this difference was only marginally significant (Table 2.5). There was no significant difference in the number of acorns dispersed more than 5 meters in urban compared to non-urban landscapes. Acorns that were dispersed were moved significantly further in 2010 compared to either 2009 or 2011 (Figure 2.16) and significantly further in non-urban compared to urban landscapes with all years pooled

(Table 2.5). While dispersal distances were consistently longer in non-urban sites, within individual years, this difference was only significant in 2010 when dispersal distances were longest (Figure 2.16).

The habitat to which acorns were dispersed was only recorded in 2010 and 2011. During those years, 287 acorns were dispersed and the cache site located (> 50 cm). The majority (74%) of dispersed acorns were moved to a single location, but a sizeable proportion of acorns were moved multiple times (2 times – 23%, 3 times – 3%, and 4 times <1%). Overall, I observed a total of 352 individual movements of dispersed acorns. Of these, the vast majority of acorns (88%, n=254) were dispersed to the same habitat type as the one from which they were taken. Of all dispersal movements, 94% of acorns removed from conifer plots were moved to conifer forest and 86% of acorns taken from oak plots were moved to oak forest. Very few acorns were dispersed from non-forest grassland plots (n=9), of these 55% were dispersed to open grassland and 44% were taken to shrub cover. Of the acorns taken from oak plots, 5% were moved to conifer cover, 4% were moved to shrub cover, and 5% were moved to non-oak deciduous tree cover. Of the acorns taken from conifer plots 3% were moved to shrub cover, 1% were moved to non-oak deciduous cover, and < 1% were moved to non-forested grassland. Only two acorns were moved from conifer cover to non-forested grassland and both were later moved back to conifer cover. These were the only acorns moved to non-forested grassland. Acorns that were dispersed multiple times and that were dispersed to different cover types from the one in which they originated were more likely to be moved longer distances (Table 2.5).

Seedling Transects

I surveyed nine non-forested grassland transects (5 urban and 4 non-urban), 23 conifer forest transects (14 urban, 9 non-urban), and 10 gap transects (8 urban, 2 non-urban). I extended six transects beyond 60 meters. The longest transect extended up to 250 meters, but the maximum distance from a nearest adult that seedlings were found was 95 meters (i.e. another adult oak was found within 95 meters of the transect).

Only two grassland transects had any seedlings and no seedlings were found more than 17 meters from the adult oak trunk in non-forested grasslands (Figure 2.17). Gap transects showed the same pattern with seedlings present up to 10 meters from the adult oak, then absent in non-forest grasslands and often present once conifer forest cover began (40-60 meters from the oak edge depending on the transect). Seedlings were also found under lone conifer trees or shrubs present in otherwise non-forested grassland. Seedlings were significantly more abundant in forested transects compared to non-forested grassland transects in the 0-10, 10-20, and 20-30 meter distance bins (Figure 2.17). Seedlings were present in forested transects up to 60 meters from the nearest adult, whereas no seedlings were found in non-forested grassland transects beyond 17 meters.

In both urban and non-urban forested transects, seedling abundance was not significantly different between distance bins up to 30 meters from the nearest adult, but was significantly lower in distance bins beyond 30 meters (30-40, 40-50, and 50-60) (Figure 2.18). In other words, seedlings were equally abundant up to 30 meters from the oak woodland edge and significantly less abundant beyond this distance. Seedling abundance was not significantly different between urban forest and non-urban forest transects.

Saplings were present in 43% of non-urban transects and 13% of urban transects. Unlike seedlings, saplings were present in non-forested grassland portions of transects (Figure 2.17). However, saplings were significantly less abundant in grassland compared to forested transects at 0-10, 20-30, and 30-40 meters from the nearest adult oak. Saplings were significantly less abundant in urban forested compared to non-urban forested transects in the 0-10 meter bin (LRT, $X^2 = 2.4673$, p-value = 0.04) (Figure 2.18).

DISCUSSION

Landscape structure had a significant effect on oak dispersal and regeneration patterns and processes. In urban landscapes, seed dispersal services were measurably inferior to those provided by animals in non-urban landscapes. In both landscape types, the presence and distribution of forest cover, and to a lesser extent shrub cover, had a strong influence on dispersal activity and subsequent patterns of seedling abundance. Finally, the cost of acorn dispersal in both landscapes was very high as the majority of acorns were consumed, few acorns were buried, and, overall, dispersal distances were short.

Effects of Urban Environment

Oak regeneration processes were measurably different in urban compared to non-urban landscapes. The stages of regeneration that differed were those controlled by animal dispersers, namely acorn handling, predation and dispersal distance. Animals handled more acorns from urban oak woodland plots. This could be positive for oak reproduction if high removal increases the number of acorns dispersed. However, I found that handled acorns in urban oak woodlands were more likely to be consumed and were dispersed shorter distances. All of these outcomes reduce the effectiveness of urban acorn dispersal services for facilitating oak regeneration.

My finding of elevated levels of seed removal are consistent with previous urban ecology research (Bowers and Breland, 1996; Shochat et al., 2004a). Several factors could theoretically lead to higher seed removal in urban landscapes: 1) higher competition among conspecifics due to a higher density of foraging individuals; 2) high competition due to food resource scarcity; 3) a lower risk of predation while foraging; 4) a limited availability of adequate caching sites (i.e. smaller forest patches) and/or 5) inherent differences in eastern and western gray squirrel behavior and ecology.

Competition for food resources should theoretically lead to higher acorn handling rates. Competition itself could be due to either a higher density of foraging individuals or greater food scarcity (or both). In general, when food is scarce, the risk of pilfering is high and squirrels expend greater energy hiding food caches leading to longer seed dispersal distances (Moore et al., 2007). In 2010, when acorn production was low (i.e. food was scarce), dispersal distances increased in both urban and non-urban landscapes. This finding indicates that squirrels in this region respond to food scarcity by taking acorns longer distances. Consequently, if food resources were scarce in urban compared to non-urban landscapes, dispersal distances should be longer in urban sites. Instead, I found the opposite. In addition, acorn production was not significantly different in urban compared to non-urban landscapes, suggesting that acorn resources are similar in urban and non-urban oak woodlands.

In contrast, previous research has found that when squirrels forage in the presence of conspecifics, they prioritize seed removal over hiding food caches and so only take seeds short distances (Hopewell et al., 2008). Consequently, the combination of higher acorn handling and shorter dispersal distances is more consistent with the hypothesis that squirrel density, rather than food scarcity, is driving the foraging and caching dynamics in urban landscapes. A meta-analysis review found that eastern gray squirrels tend to live at higher densities in smaller forest fragments. Home range size for eastern gray squirrels ranged from approximately 2.17 to 10 hectares depending on forest fragment size (Koprowski, 2005). In urban areas, home ranges of female relatives often overlap and communal nests of two to nine eastern gray squirrels are common (Koprowski, 1996). In contrast, overlap between female eastern gray squirrels on JBLM was extremely low (5.7% of home range size). Overlap between female western gray squirrels was also low (mostly <10%) although overlap between western males and males and females was high (110-205%) (Johnston, 2013).

While increased foraging competition can lead to shorter dispersal distances, differences in dispersal distance could also be explained by the inherent behavioral differences between eastern and western gray squirrels. On JBLM, the home ranges of western gray squirrels are on average larger than those of eastern gray squirrels (Johnston, 2013). Home range size is good predictor of dispersal distance for mammals, suggesting that home range size is a reasonable predictor of vagility (Bowman et al., 2002). It is therefore possible that, all else being equal, the less vagile eastern gray squirrels would disperse acorns shorter distances. If this is the case, the presence of eastern gray squirrels and lack of western gray squirrels in urban areas alone should result in shorter dispersal distances. This mechanism however, would not explain the increased acorn handling in urban landscapes.

Predation risk can also affect foraging dynamics. All else being equal, seed removal is generally higher in safe compared to risky habitats (Bednekoff, 2007; Kotler and Brown, 2007). In support of this theory, in both urban and non-urban landscapes, I found that acorn handling was significantly higher under conifer forest compared to non-forested grassland habitats. Removal from plots located under oak canopy was intermediate between these two habitat types, likely due to both the presence of canopy cover and the availability of acorns (which fell naturally from oak trees) under oak canopy. Both eastern and western gray squirrels in this region use forested areas and forest canopy connectivity is an important predictor of both nesting site and resource use areas for both species (Johnston, 2013). Consequently, it is not surprising that removal was extremely low in the non-forested grassland plots in both landscape types. There was no significant difference in removal from open grassland plots in urban versus non-urban sites, indicating that squirrels eschewed these habitats equally in both landscape types. However, this is not a definitive test of the predation hypothesis because grassland habitats provide squirrels with neither food nor safety on a regular basis, and so squirrels have little incentive to venture into these habitats to search for food regardless of predation risk.

Another factor that may affect both squirrel density and dispersal distance is the amount of forest cover present at each site. Urban and forest land covers are negatively correlated and there was significantly less conifer forest cover at the urban compared to non-urban sites. Forest fragmentation can lead to a higher density of individuals as animals "pack" themselves into remaining forest fragments (Koprowski, 2005). In addition, because squirrels prefer to cache acorns under forest canopy, smaller forest patches may lead to shorter dispersal distances. I believe this is unlikely because in all urban sites in my study, sufficient conifer cover was available that acorns could have been dispersed longer distances than observed, without the dispersal agent having to leave conifer cover. Alternatively, it is possible that alternative food resources in urban areas reduced food scarcity (Parker and Nilon, 2012) and subsequently reduced the benefit of dispersing acorns longer distances in urban landscapes.

Reduced dispersal services could have a significant impact on oak regeneration. Due to higher acorn consumption rates, significantly fewer acorns produced seedlings in the urban sites compared to the non-urban sites overall (Table 2.2). This finding suggests that over time seedlings should become less abundant in urban oak woodlands. However, in contrast to this finding, data from both vegetation surveys (Michalak, 2011) and seedling transects (Figure 2.18) found no significant difference in oak seedling abundance between urban and non-urban landscapes.

Effects of Habitat Composition

Canopy and understory type had a significant impact on dispersal and regeneration processes. The effect of canopy cover was the most consistent across years and landscape type. Acorn handling, an indication of acorn disperser activity, was highest in conifer forest plots, moderate in oak plots and lowest in non-forest grassland plots (Figure 2.4). Differential acorn abundance likely led to higher removal from conifer forest compared to oak forest, as naturally occurring acorns were present under the oak canopy. Both eastern and western gray squirrel habitat use is tightly correlated to forest canopy cover (Johnston, 2013), explaining the very low level of acorn handling from non-forest grassland plots. The acorns that were removed from grassland plots were possibly taken by other rodents such as mice. Tunnels were found crossing the plots and several tagged acorns were found dragged into tunnels. The walnut baits left in hair snag traps near non-forested grassland plots were not removed.

Understory type also affected removal. Overall, removal was significantly lower from plots with grass compared to shrub or open herb understory. Even within oak canopy plots alone, removal was higher in those with shrub compared to those with grass understory (Figure 2.4).

Grass in this region creates dense mats which could be difficult for squirrels to move through. In contrast, shrubs such as snowberry (*Symphocarpus alba*) provide dense cover from predators but also a bare soil surface beneath the shrub canopy, which may facilitate foraging. There was no significant difference between conifer forest plots with shrub versus open herb understory. At least on JBLM, western gray squirrels have been found to prefer habitats with open herb understory while eastern grays prefer areas with shrub understory (Johnston, 2013).

The proportion of remaining acorns (i.e. those not taken by seed dispersers/predators) that germinated was significantly higher under oak canopy (Table 2.2, Figure 2.9). Acorns under oak canopy may benefit by being covered with fallen leaves at the end of autumn. Desiccation is a significant source of acorn mortality (Stein, 1990) and acorns buried beneath leaf litter have a higher chance of survival (Fuchs et al., 2000). In addition, seedlings produced in areas with shrub cover in 2009 were more likely to survive to a third year than those produced in grassland areas (Table 2.2 and Supplementary Table 2). Other studies have found that shrubs facilitate oak regeneration (Callaway, 1992; Callaway and Davis, 1998; Gómez-Aparicio et al., 2004; Rousset and Lepart, 1999). Overall, observed seedling abundance in this study area is significantly lower in shrub understory, but sapling abundance is higher, suggesting that the few acorns that do survive in shrub understory may have a recruitment advantage (Michalak, 2011).

Finally, forest cover appears to play an important role in facilitating dispersal of oak acorns. Vegetation surveys in the study area found that seedlings are significantly more abundant under conifer canopy compared to non-forested grasslands (Michalak, 2011). Data from seedling transects corroborate this finding as seedlings were virtually absent in non-forested grasslands but regularly present up to 40 meters and found up to 95 meters from the nearest adult in forested areas (Figure 2.17). The most striking example of this phenomenon is seen in gap transects which started at the oak/grassland edge, extended through non-forest grasslands and into conifer forest. Seedlings were present under oak canopy and perhaps a few meters beyond, but then absent throughout the non-forest grassland and often present again once conifer forest resumed. Several studies have found that jays and rodents prefer to cache acorns under forest canopy (Fuchs et al., 1999). In this study, dispersed acorns were preferentially cached under forest cover.

Characteristics of Dispersal Services

Dispersers handled a majority (68%) of the acorns in this study. Handling rates for plots located under oak canopy ranged from 40-60% in non-urban sites and 60-81% in urban sites depending on the year. These rates are within the range (53-100%) observed by Fuchs (2000) in *Q. garryana* woodlands on Vancouver Island, Canada. However, these rates are lower than similar studies of acorn handling of other oak species, which have found near 100% removal (Gómez et al., 2008; Xiao et al., 2006; Zhang et al., 2008). This moderate handling rate meant that 20-60% of acorns were left in place, depending on location and year, and therefore had the opportunity to germinate and produce seedlings.

Germination rates were significantly higher under oak canopy compared to both conifer and grassland plots (Figure 2.8, Table 2.2) suggesting that condition under oak canopy are favorable for germination, perhaps due to fallen oak leaves protecting acorns from desiccation. In addition, data from vegetation surveys in this area indicate that oak seedling abundance is highest under oak canopy, as opposed to conifer or in open grasslands (Michalak, 2011). Research has shown that in other oak systems, seedling abundance is high under oak canopy, but seedling growth and recruitment to the sapling stage under adult oaks are limited (Brudvig and Asbjornsen, 2008; Callaway and Davis, 1998). Brudvig and Asbjornsen (2008) found significantly lower growth of *Q. alba* seedlings under adult oak canopy compared to canopy gaps. While the authors suggest that shading may be a factor reducing seedling growth, preliminary results from canopy thinning experiments found increased seedling mortality in thinned plots, although the seedlings that survived exhibited greater growth. *Q. garryana* is generally considered shade intolerant (Stein, 1990). However, Fuchs et al. (2000) found that seedling survival of *Q. garryana* in B.C. Canada, was not related to overstory vegetation. Through my experimental plantings, I found that acorns planted in non-forested grasslands readily produced seedlings. Initial survival rate for these seedlings was comparable to that of seedlings produced under either oak or conifer forest cover (66%, 63%, or 53% respectively). Consequently, while seedling production may be high under oak canopy, recruitment potential may be low.

Handling by dispersers potentially confers three significant benefits to oak acorns: 1) acorns are buried which should reduce post-dispersal mortality, which increases germination and seedling production (Fuchs et al., 2000); 2) acorns that are dispersed away from the parent tree should have increased survival and recruitment success by escaping density dependent mortality near the parent tree (Janzen, 1970); and 3) dispersal allows acorns to colonize currently unoccupied but suitable habitat (Trakhtenbrot et al., 2005). In my study, I found mixed evidence for all three benefits. While a significant number of acorns were dispersed, few were buried, dispersal distances were short and the consumption rate of dispersed acorns was high. These findings suggest that the cost of dispersal is high. Despite these high costs, seedling densities observed in transect surveys suggest that successful dispersal to approximately 30 meters into conifer forest adjacent to oak stands is common in this study area (Figure 2.17).

Experimentally planting acorns did significantly decrease seed removal, and increase germination and seedling production (Figure 2.4, Figure 2.8, and Figure 2.10). In total, 17% of remaining planted acorns produced seedlings, significantly more than either surface or tagged acorns. Other studies have found that planting acorns significantly increases germination and seedling production (Fuchs et al., 2000). However, animals that handled the tagged acorns buried very few (6%) in either landscape (n=40 urban, n=38 non-urban). This percentage is lower than the range found in other studies (7.5% of *Q. ilex* in Spain (Gómez et al., 2008); 50% of *Q. ilex* in Spain (Munoz and Bonal, 2007); 17-36% of *Q. liaotungensis* and *Q. serrata* (Zhang et al., 2008). In urban landscapes, 92% of buried acorns were consumed and in non-urban landscapes 48% were consumed. The urban rate of consumption is within the range documented (63% for *Q. ilex* in Spain (Gómez et al., 2008), 90% for *Q. ilex* in Spain (Munoz and Bonal, 2007); 97-98% *Q. liaotungensis* and *Q. serrata* (Zhang et al., 2008), while the non-urban rate is slightly lower. These findings suggest that dispersers in this system bury acorns less often than has been found in other oak systems, but the consumption rate is moderate to low depending on the landscape type. It is possible that dispersers bury un-tagged acorns at a higher rate, although the studies cited above all used tags to track acorn dispersal.

Dispersal distance is important not only to increase survival but also to allow oaks to colonize new locations. The ability to move long distances is increasingly important as the climate changes because dispersal is necessary in order for plants to track changing climate conditions (Trakhtenbrot et al., 2005). In this study, acorns were moved very short distances. A moderate percentage of acorns (36% urban, 32% non-urban) were dispersed more than 50 cm, but the majorities of these were consumed. Only 6% of tagged acorns were moved more than 5 meters, a conservative estimate of the minimum distance needed to be dispersed beyond the parent oak canopy. However, 2% of acorns traveled between 10 and 30 meters, and a few acorns were recovered beyond 30 meters (7 acorns <1%). All but two of these dispersed acorns were taken into either oak or conifer forest. I found that acorns can germinate and produce seedlings in both habitat types (Figure 2.10, Figure 2.11). Despite this finding, previous research suggests that survival and recruitment of oak seedlings in either oak or conifer forest may be limited (Brudvig and Asbjornsen, 2008; Callaway and Davis, 1998; Devine and Harrington, 2006). Therefore, although seedlings may be readily produced under both oak and conifer forest cover, over the long term, these seedlings may have a limited opportunity to survive to the sapling and adult stages in these habitats.

High predation and low caching rates suggest that dispersal services in both landscapes are at best very costly, and at worst ineffective. However, contrary to this conclusion, my transect data show that seedlings are equally abundant under conifer forest up to 30 meters from oak canopy (Figure 2.18). In addition, seedlings were found forested areas up to 95 meters from the nearest adult oak. One explanation for this apparent discrepancy is that compared to the abundance of acorns available, my experimental sample is infinitesimally small. If acorn-dispersing animals move even 1% of all acorns produced between 10 and 30 meters each year, this could result in a significant number of seedlings accumulating beyond the oak canopy edge.

Alternatively, there are several possible reasons that my study may be underestimating the value of dispersal services in this area. First, dispersers may have treated tagged acorns differently. Squirrels are keenly able to detect variation in acorn quality (Steele et al., 2001), and may have considered the tagged acorns to be damaged and therefore less likely to store over winter. Less valuable food items are generally dispersed shorter distances and perishable food items are consumed faster (Moore et al., 2007).

Secondly, the seed tracking method used in this study potentially underestimates dispersal distance, germination and survival (Xiao et al., 2006). I recovered 95% of the initial acorns in the study at the end of the fall season and 87% by the end of the spring season, an extremely high proportion compared to other similar studies (Gómez et al., 2008; Xiao et al., 2006; Zhang et al., 2008). Nevertheless, increasing the search radius increases search area significantly, making it more difficult to find acorns that are dispersed longer distances. A total of 72 acorns (5%) were not recovered by the end of the fall season. Sixteen of these missing acorns were due to the acorns being separated from the tag. It is unlikely that these sixteen acorns were dispersed in a way that was systematically different from the rest of the tagged acorns that year. This leaves 55 (4%) acorns that were lost and were likely dispersed differently from the recovered sample. These missing acorns could have dispersed beyond my search radius. This possibility is supported by the fact that by far the greatest number of acorns was lost in 2010 when dispersal distances were longest. However, it is also possible that these acorns were taken into trees or down tunnels. I relocated one acorn that had been partially dragged into a tunnel. Another tag reappeared under a tree near one of my plots with the acorn removed suggesting that it might have been stored in the tree during the week I first searched for it, and later eaten and the tag dropped. While more acorns were lost in the spring (an additional 8% of my sample), it is likely that a significant proportion of these were lost because they were moved a short distance and buried under fallen leaves and debris over winter. I do not expect that these acorns were all taken beyond 100 meters, but it is possible that some were and this would lead me to underestimate dispersal distances.

Thirdly, in this study, I did not restrict access to my plots and therefore am not able to determine definitively which species visited my plots and dispersed acorns. The dispersal patterns I observed are consistent with known activity patterns of eastern and western gray squirrels. The dispersal distances observed are within the range recorded for other rodent dispersal studies (Gómez et al., 2008; Xiao et al., 2006; Zhang et al., 2008). Additionally, I found low acorn handling and short dispersal distances at site 189 where gray squirrels were largely absent. However, Douglas squirrels and mice were present and could have also handled and dispersed acorns. Douglas squirrels are larder hoarders, which mean that they cache multiple acorns in the same location. I found one tagged acorn buried in such a cache at one site used in 2009. However, all other tagged acorns were buried singly. I occasionally found tunnels dug through my acorn planting locations suggesting that mice were responsible for some predation and likely short dispersal distances. In particular, in the open grassland locations, I occasionally found tagged acorns dragged into tunnels which had been burrowed through the grass. I placed hair snag traps near my grassland sites with comparatively high acorn handling. The walnuts used as bait in the traps at these locations were not taken, reducing the likelihood that squirrels were foraging in the area. I am not aware of an exclusion technique that could permit gray squirrels access but not mice or Douglas squirrels.

Steller's jays are another important disperser species for *Q. garryana* (Fuchs et al., 1999; Larsen and Morgan, 1998). Observations of Steller's jays have found that these birds will move *Q. garryana* acorns up to 600 meters from adult trees, possibly up to 1 kilometer (Fuchs et al., 1999). Studies of jay dispersal of other heavy seeds have estimated maximum dispersal distances of about 550 meters for *Quercus ilex* and *Q. suber* (Pons and Pausas, 2007), 1 km for holm-oak (*Q. ilex*) dispersed by the European jay *Garrulus glandarius*, (Gómez et al., 2008), 4 km for smaller Beechnuts (*Fagus grandifolia*) dispersed by Blue jays (*Cyanocitta cristata*) (Johnson and Adkisson, 1986), and ~1 km for *Q. palustris* acorns dispersed by Blue jays (Darley-Hill and

Johnson, 1981). Capturing these long distance dispersal events was not possible given the seed tracking method used here. As mentioned earlier, it is possible that lost acorns were dispersed outside my search radius, potentially by jays. Dispersal distances, burial rates, and consumption rates by jays may differ from squirrels and distinguishing between dispersal patterns of jays and squirrels is an important area for further research.

Variable acorn production in each of the three years included in the study had a significant and consistent impact on dispersal and regeneration processes. Acorn production was negatively correlated with acorn handling, predation and dispersal distance and positively correlated with germination and seedling production (Figure 2.4, Figure 2.8, and Figure 2.10). When ambient food is abundant, simple probability suggests that the likelihood that a forager would remove acorns from experimental plots should be lower. Similarly, abundant food should also decrease the probability of any individual acorn being consumed and therefore lower the predation rate. Specifically, in 2009 when acorn production was high, acorn handling, dispersal, and predation were low. Not surprisingly, rates of germination and seedling production were significantly higher overall during this year as significantly fewer acorns were handled or eaten. This finding is consistent with the seed predator satiation hypothesis, which states that oak trees produce a mast crop of seeds to overwhelm seed predators (McShea, 2000). However, a higher proportion of the remaining acorns (i.e. those not handled by seed predators) germinated and produced seedlings in this year compared to other years. This finding suggests that ambient conditions in 2009 were particularly favorable for seedling production. The factors driving acorn masting are poorly understood (Johnson et al., 2009; Peter and Harrington, 2002), but my findings suggest that, in this case, masting at least coincided with conditions that were particularly favorable for reproduction.

Although seedling production was high, dispersal distances in 2009 were short. Only 1% of tagged acorns were moved farther than 5 meters (5 out of 361) and the longest, recorded, dispersal event was 10 meters. In contrast, in 2010 when acorn production was low, seedling production was also lower, but dispersal distances were longer (10% or 59 out of 540 tagged acorns dispersed > 5 meters, longest recorded dispersal event of 100 meters). There has been disagreement surrounding how seed production should influence dispersal distances, but other studies have found that abundant seed production reduces the cost of pilferage to caching rodents and therefore favors shorter dispersal distances in mast years (Gómez et al., 2008; Moore et al., 2007). Seedling production was moderate in 2011, and measures of dispersal and regeneration processes fell between the extremes of 2009 and 2010. However, seedling production was not significantly different between 2010 and 2011, and dispersal distances were not significantly different between 2009 and 2011. These findings suggest that mast years result in high seedling production, but limited dispersal. In contrast, seeds are moved long distances in years of low seed production, but cached seeds are more likely to be eaten and less likely to produce seedlings.

Dispersal theory states that seeds that move the longest distances have the highest probability of surviving (Janzen, 1970). Unfortunately, tagged acorns produced few seedlings and were significantly less likely to produce seedlings than un-tagged surface acorns. This suggests that the tagging process, which damages the acorn, may inhibit seedling production, although there was no significant difference in germination between tagged and surface acorns. Consequently, I could not determine whether longer dispersal distances lead to a higher seedling production probability as is theoretically expected.

CONCLUSIONS

Overall, landscape structure, including both landscape type (urban versus non-urban) and the amount and spatial arrangement of forest cover, appears to play a significant role in driving oak regeneration patterns by influencing the behavior and composition of the animal community. Specifically, regeneration stages controlled by acorn-dispersing animals differed significantly between urban and non-urban landscapes. The animal dispersal community available to oaks in urban landscapes appears to be less effective, as acorns in urban environments are more likely to be eaten and are dispersed shorter distances. However, inter-annual variation in acorn production affected all stages of reproduction and potentially over-rides differences between urban and non-urban oak reproduction. That is, in years of high acorn production, seed predators are satiated and seedling production was high in both urban and non-urban oak woodlands. These years may be the most important for oak reproduction, although perhaps not for dispersal. In fact, prior research has found that observed oak seedling abundance did not differ between urban and non-urban sites (Michalak, 2011). It may be that in the case of *Q. garryana*, variable acorn production, a strategy that oaks evolved to counteract seed predation pressure in native landscapes, is sufficient to mitigate the increased predation pressure present in urban landscapes. In other words, *Q. garryana* reproduction in urban parks appears to be resilient to altered ecosystem processes created by the urban environment. This case study illustrates the complexity of urban impacts on ecosystem functions and highlights the need for a larger body of urban natural history knowledge in order to improve urban biodiversity conservation practice.

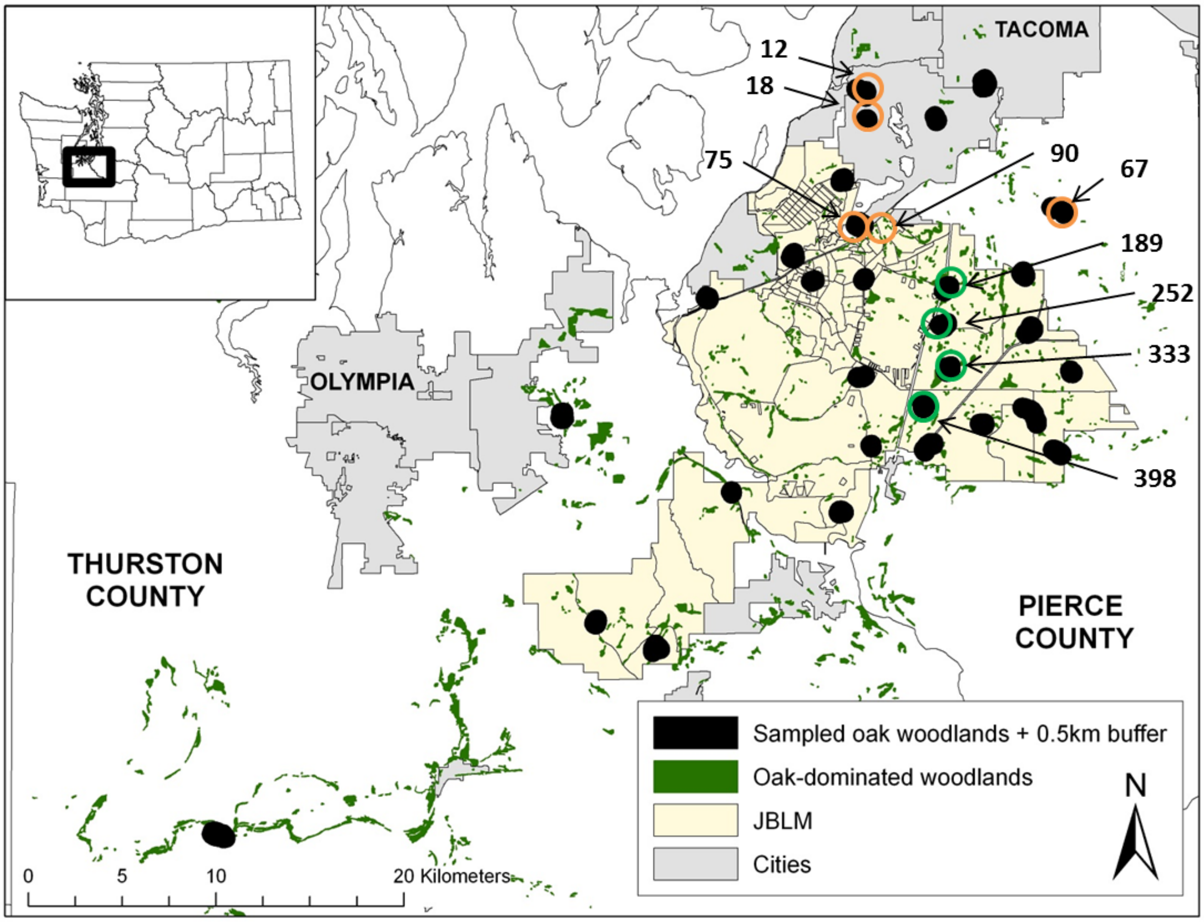

Figure 2.1. The study region. Oak dominated woodlands are shown in green. Woodlands highlighted with black were sampled for stand structure in 2009 (Michalak, 2011). Areas circled in orange indicate the location of urban oak woodland sites and areas circled in green indicate the location of non-urban oak woodland sites used to study dispersal processes.

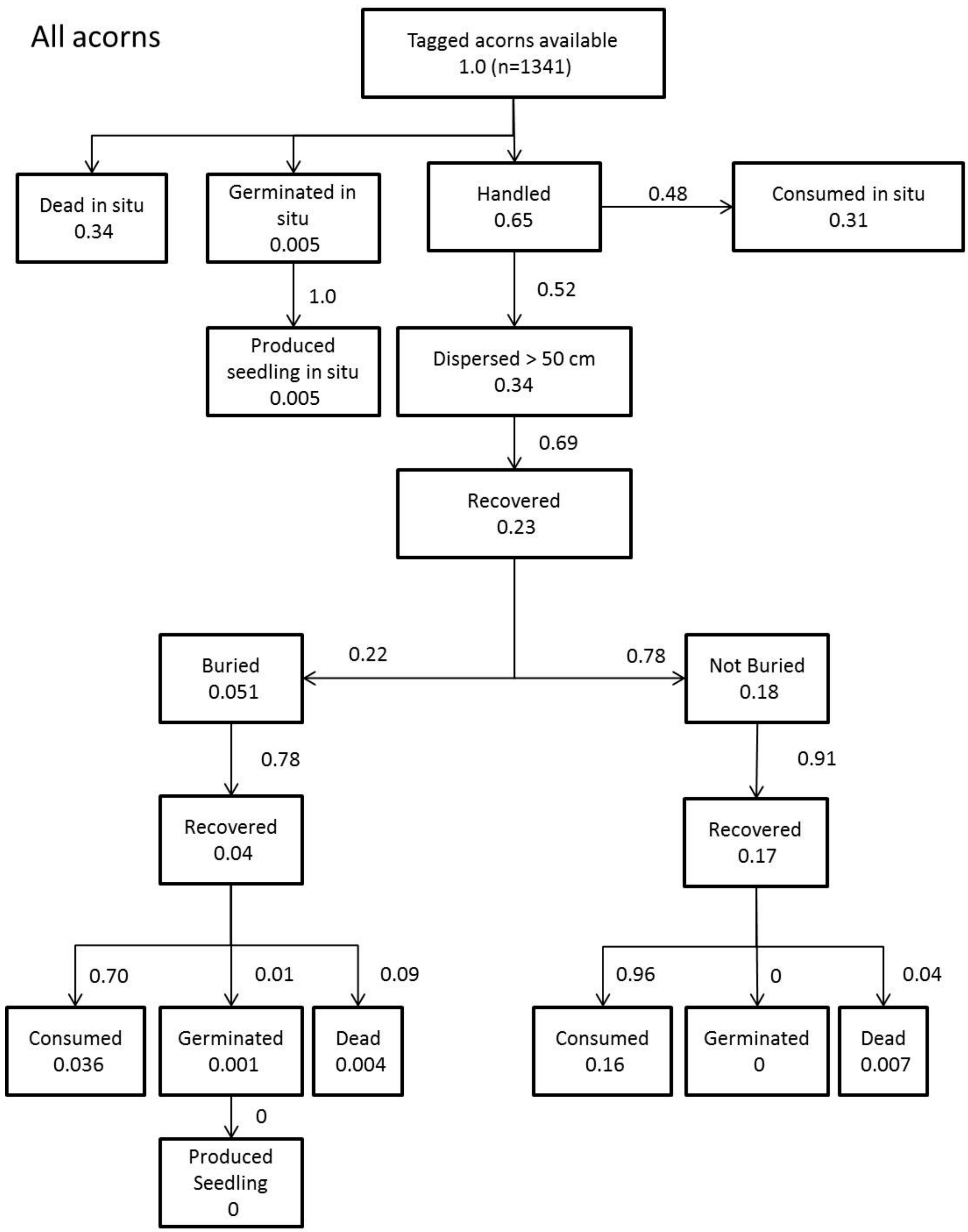

Figure 2.2. Diagram of acorn fates showing the proportion of acorns moving from one stage to the next (transition probabilities, numbers next to arrows) and the proportion of the initial experimental acorn crop at each stage (values within boxes).

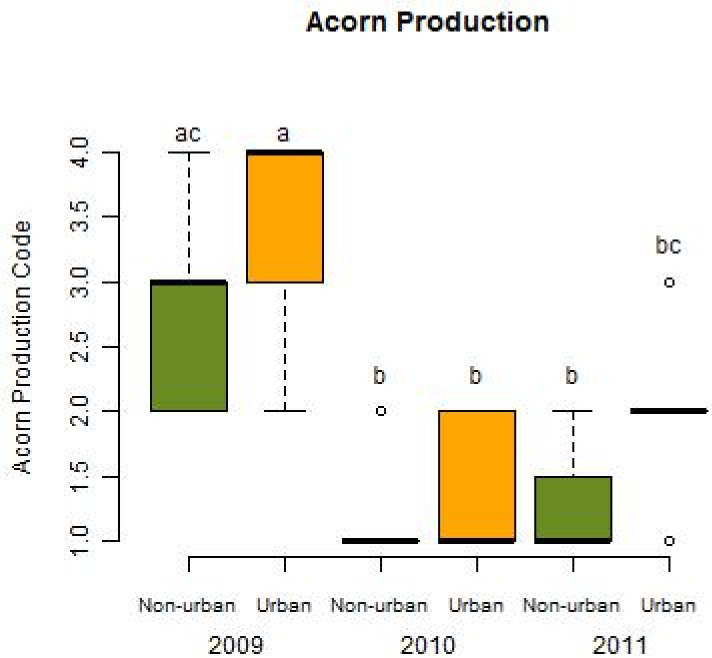

Figure 2.3. Acorn production by year and landscape type (urban/non-urban). 1 = not producing (no acorns found), 2 = light producing (one or more acorns found after some searching), 3 = moderate producing (acorns visible all around the tree, but born singly), 4 = high producing (acorns visible in clusters all around the tree). Boxplots with the same letter are not significantly different at $\alpha < 0.05$ after pairwise comparisons. Acorn production index methods developed by Peter and Harrington (2002).

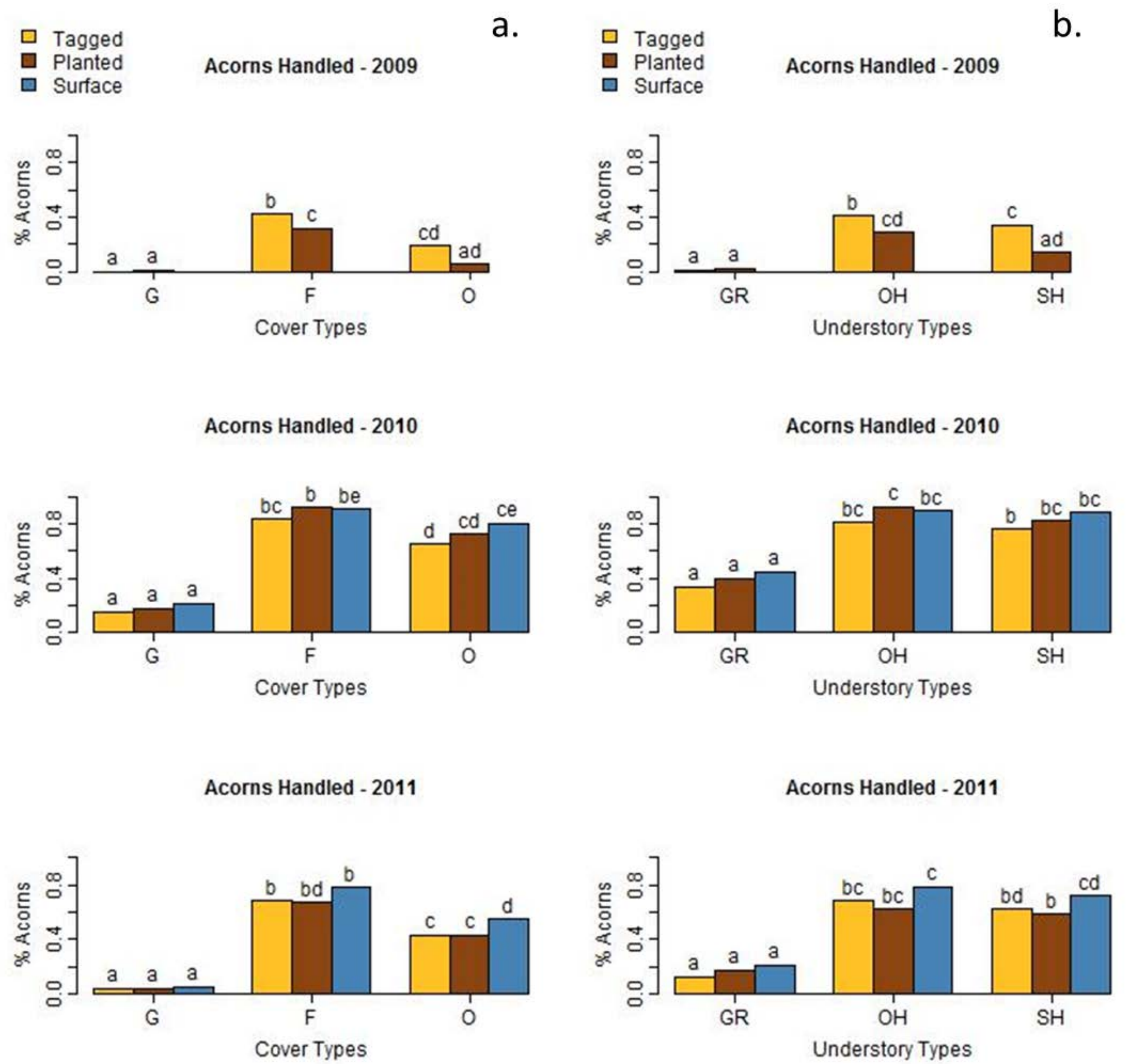

Figure 2.4. Acorn handling by treatment and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Surface treatment not used in 2009. Bars with the same letter are not significantly different at α < 0.05 after pairwise comparisons.

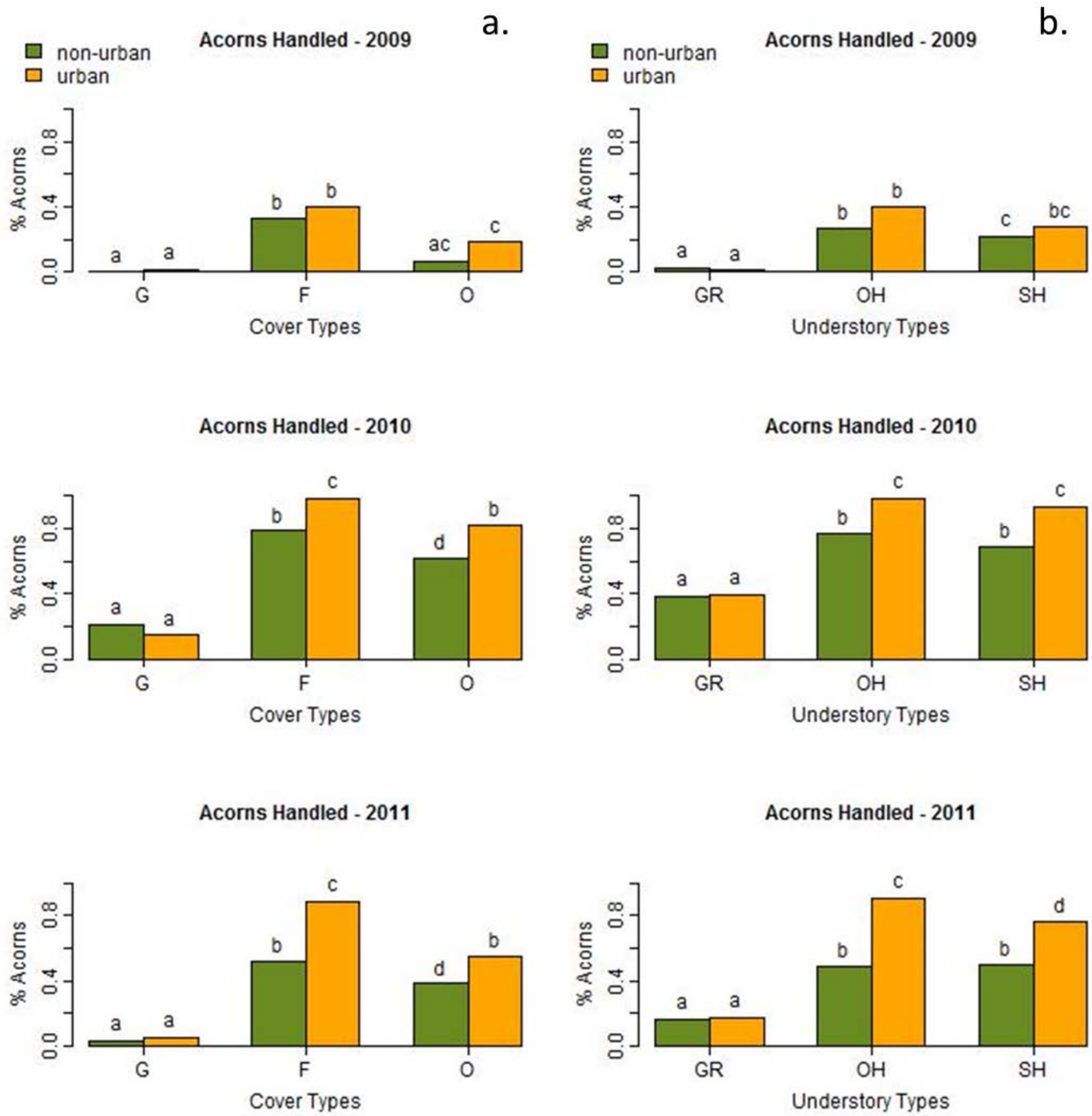

Figure 2.5. Acorn handling by landscape (urban/non-urban) and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Bars with the same letter are not significantly different at α < 0.05 after pairwise comparisons.

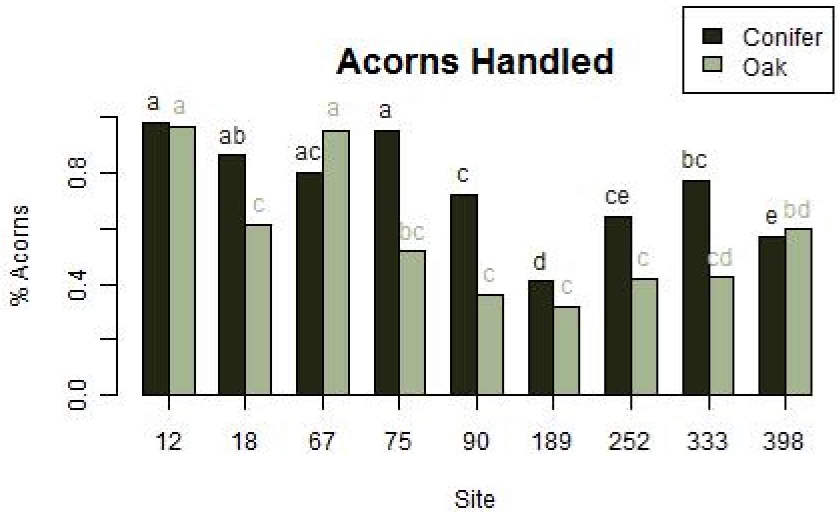

Figure 2.6. Acorn handling by canopy type (oak/conifer) and site. Sites 12 – 90 are urban oak woodland sites and 189 – 398 are non-urban sites. Letters indicate significant differences in the number of acorns handled *within* each cover type. Comparisons between cover types are not shown. A concurrent study of eastern and western gray squirrels was conducted also using sites 189 – 398. This study found that both squirrel species rarely used site 189 (Johnston, 2013). This figure shows that significantly fewer (at $\alpha < 0.05$) acorns were handled in conifer plots in site 189 compared to conifer plots in all other sites. Acorn handling in oak plots in 189 was also low, although only significantly different from sites 12, 67, and 398. See Figure 2.1 for a map of site locations within the study area. Table 2.6 provides further details on site characteristics.

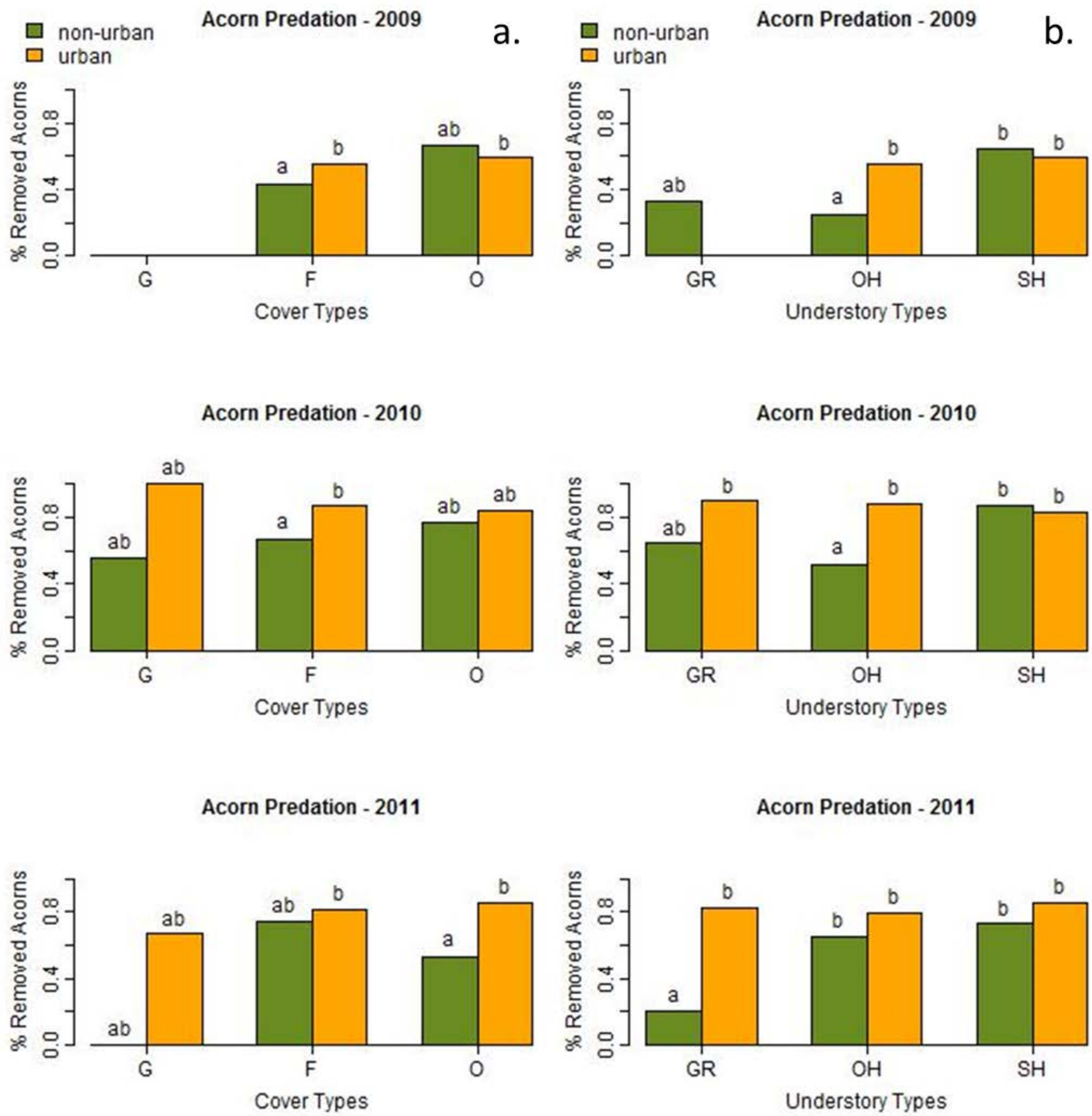

Figure 2.7. Acorn predation (% of handled, tagged acorns that were consumed) by landscape (urban/non-urban) and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Bars with the same letter are not significantly different at α < 0.05 after pairwise comparisons.

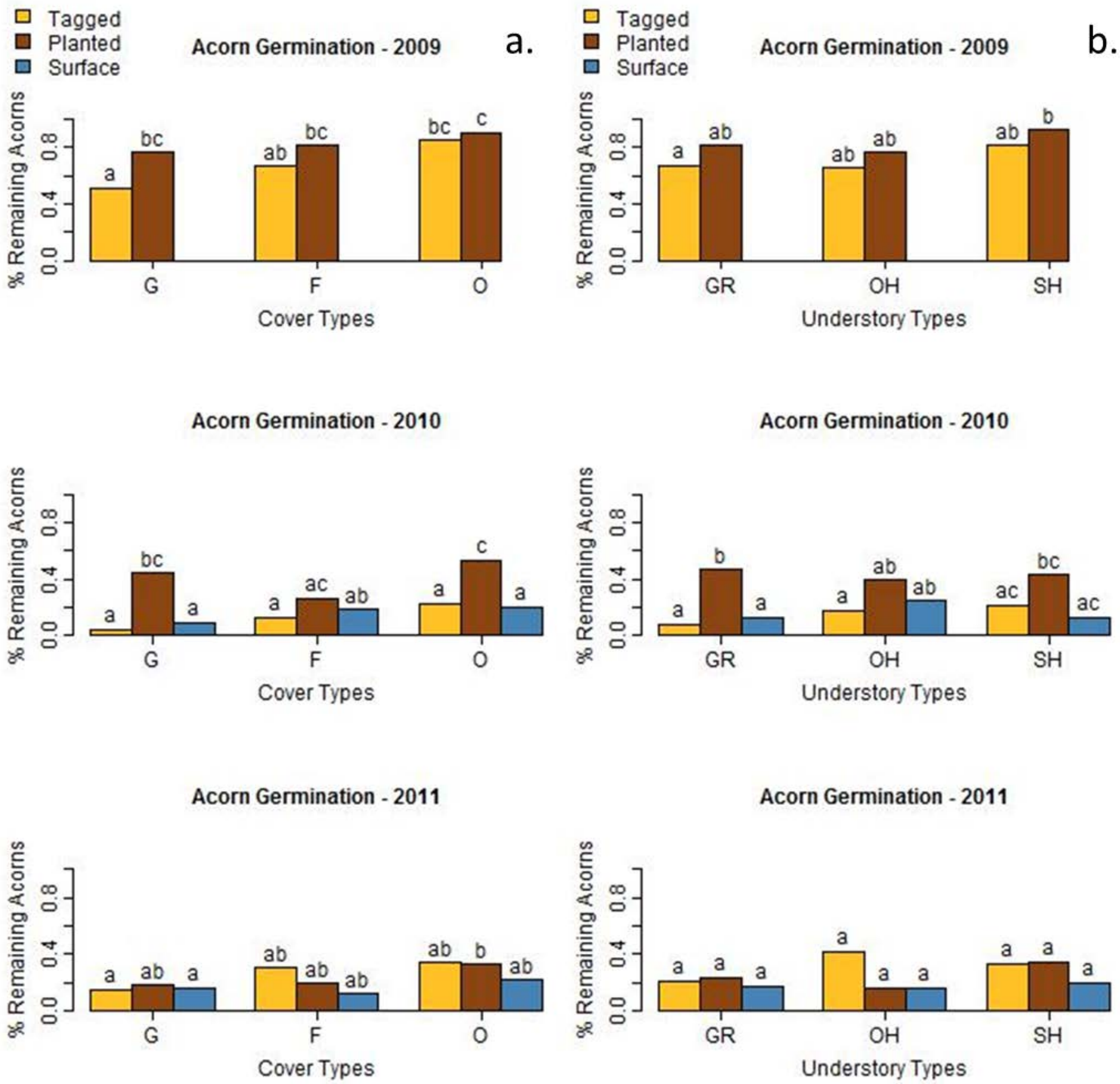

Figure 2.8. Germination rate (% of remaining acorns that germinated) by treatment and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Bars with the same letter are not significantly different at $\alpha < 0.05$ after pairwise comparisons.

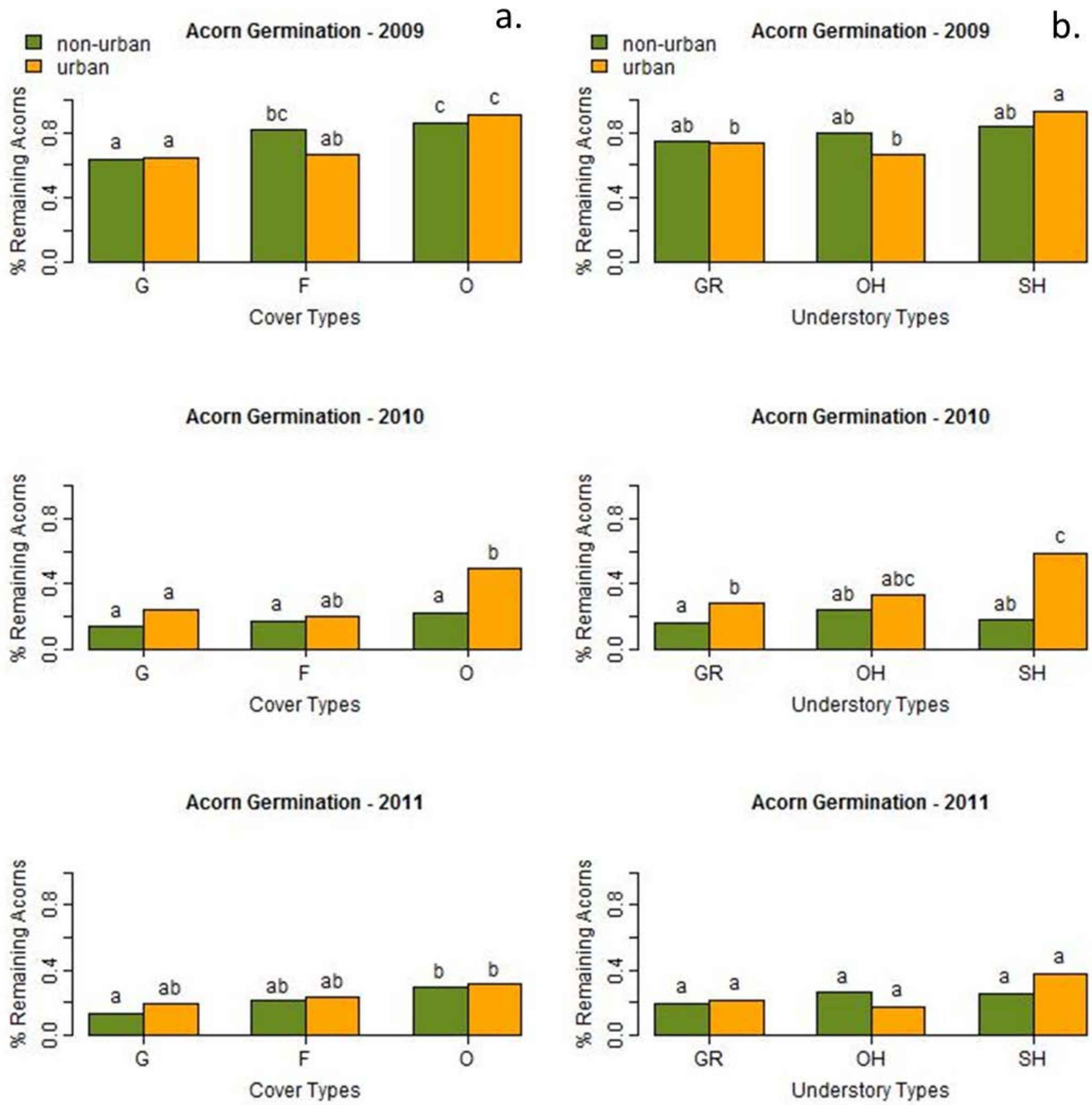

Figure 2.9. Germination rate (% of remaining acorns that germinated) by landscape (urban/non-urban) and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Bars with the same letter are not significantly different at $\alpha < 0.05$ after pairwise comparisons.

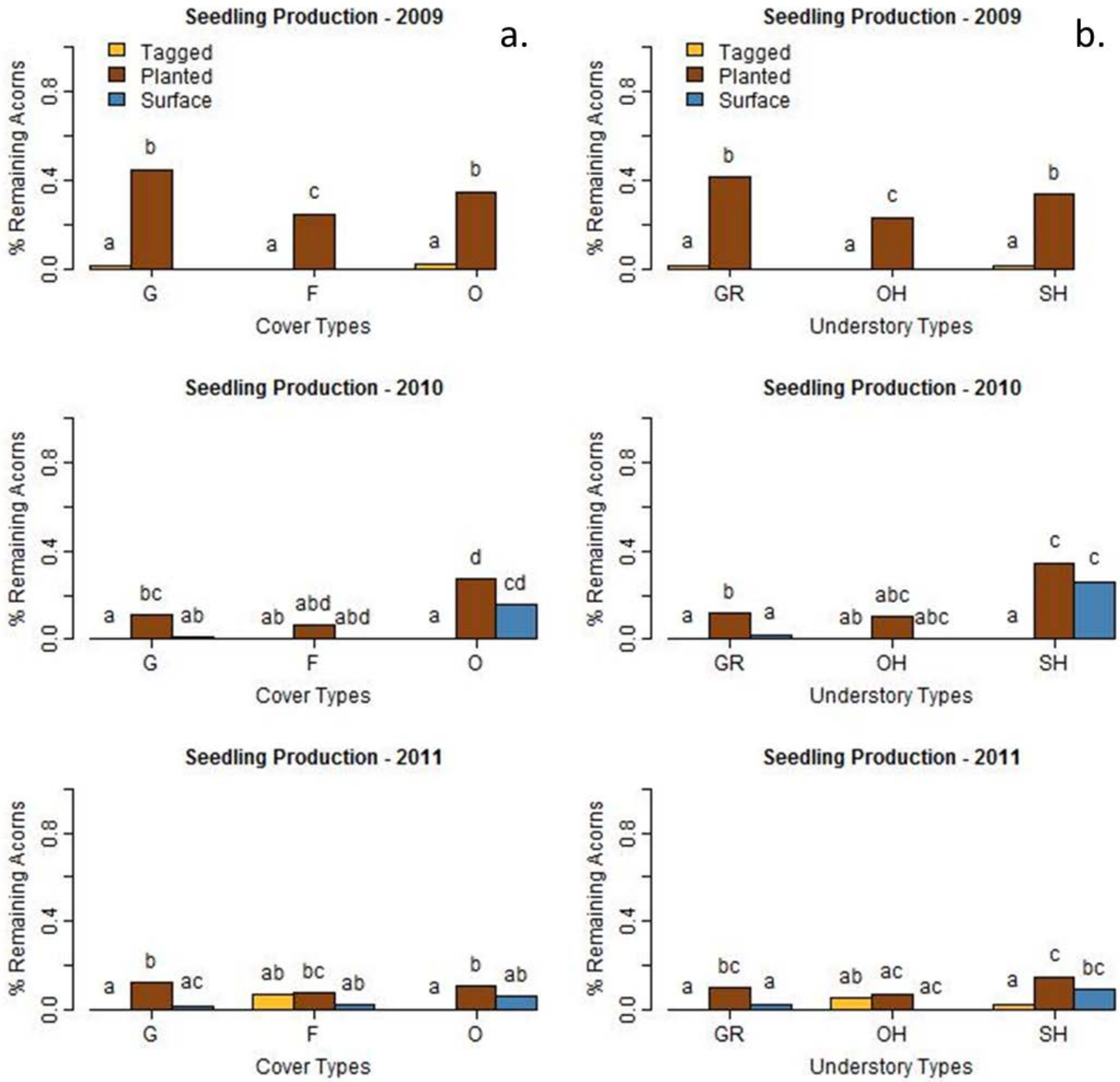

Figure 2.10. Seedling production rate (% of remaining acorns that produced seedlings) by treatment and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Bars with the same letter are not significantly different at α < 0.05 after pairwise comparisons.

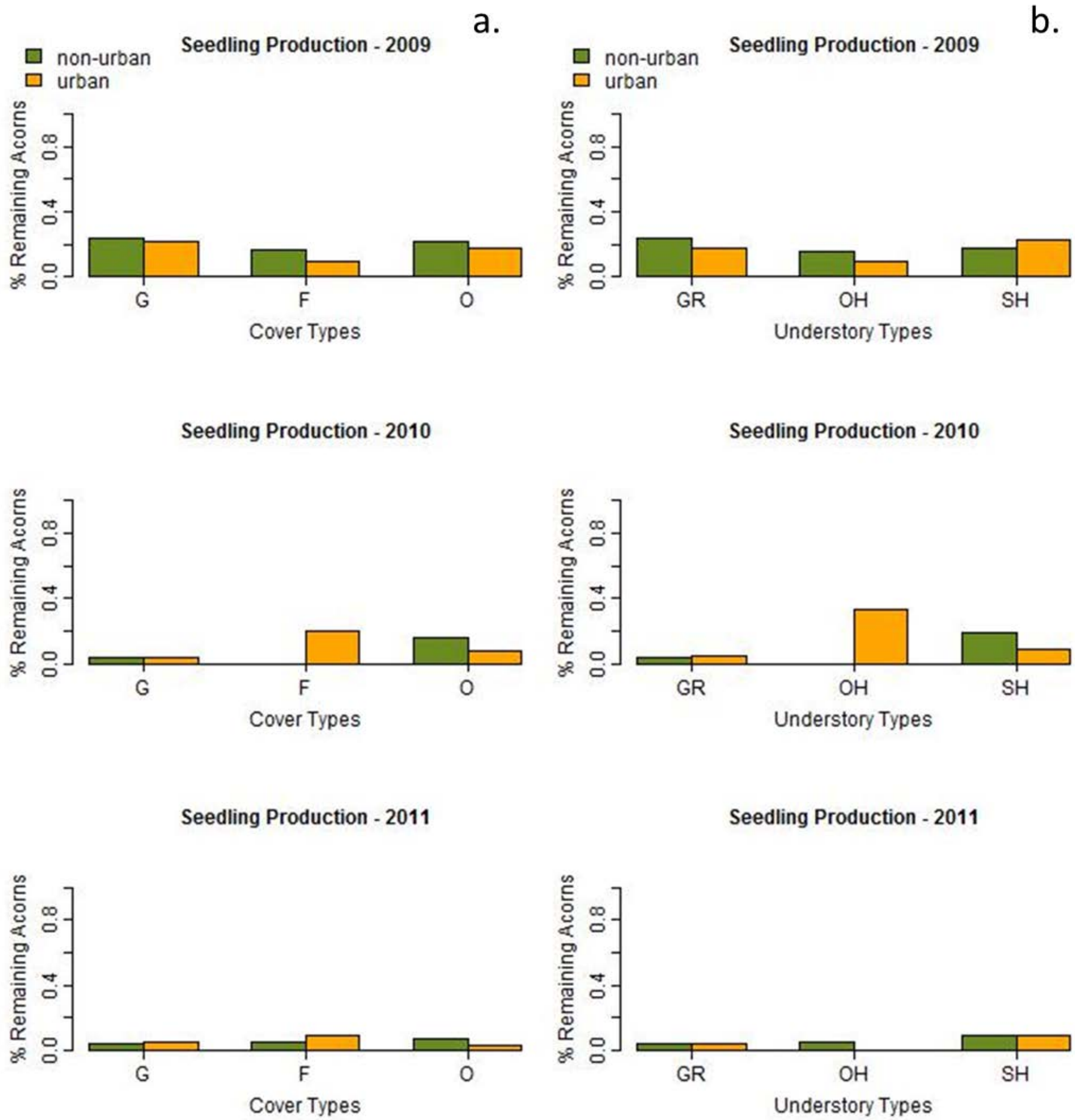

Figure 2.11. Seedling production rate (% of remaining acorns that produced seedlings) by landscape (urban/non-urban) and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. There were no significant differences in seedling production between urban and non-urban sites within cover types.

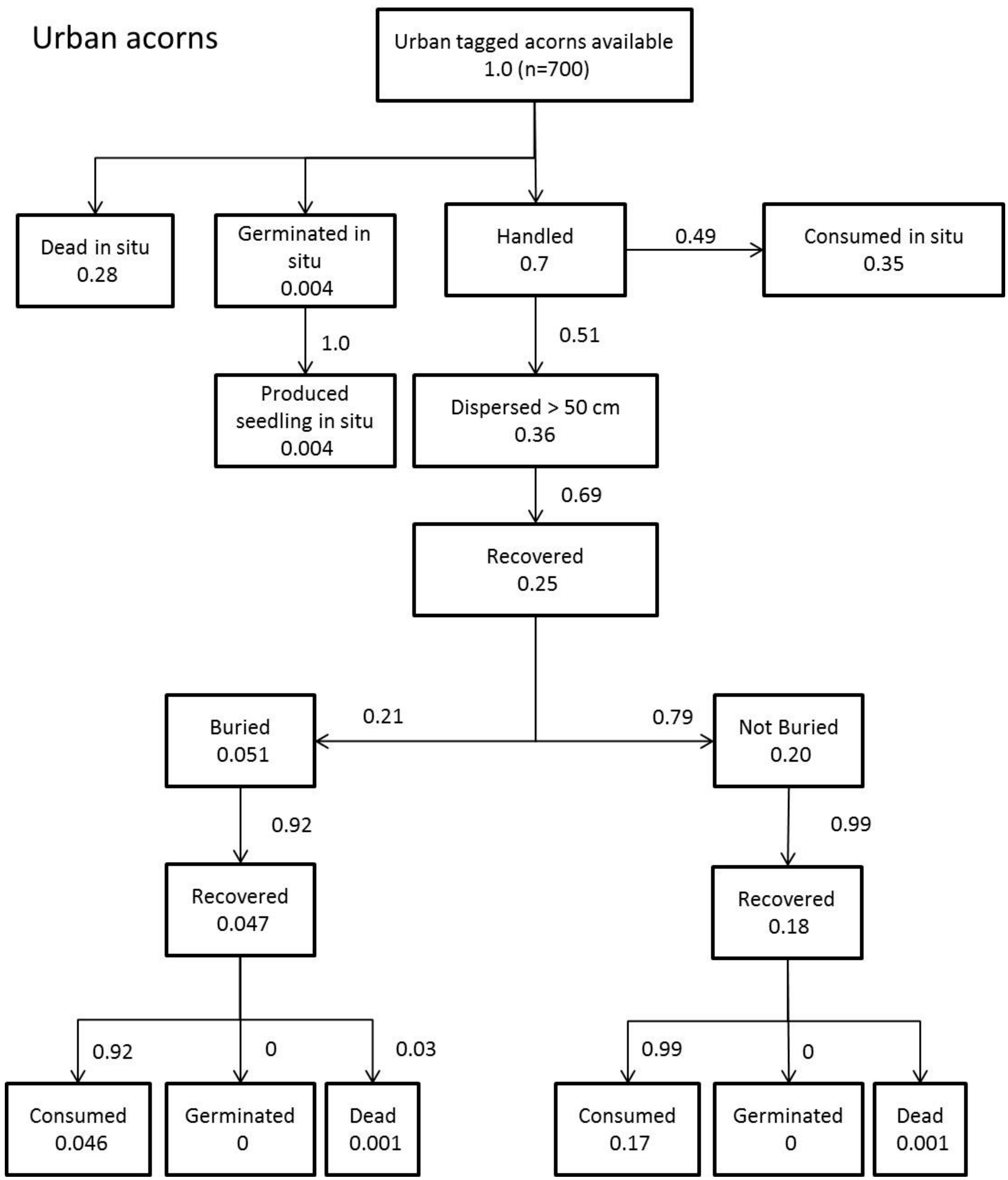

Figure 2.12. Diagram of urban acorn fates showing the proportion of acorns moving from one stage to the next (transition probabilities, numbers next to arrows) and the proportion of the initial experimental acorn crop at each stage (values within boxes).

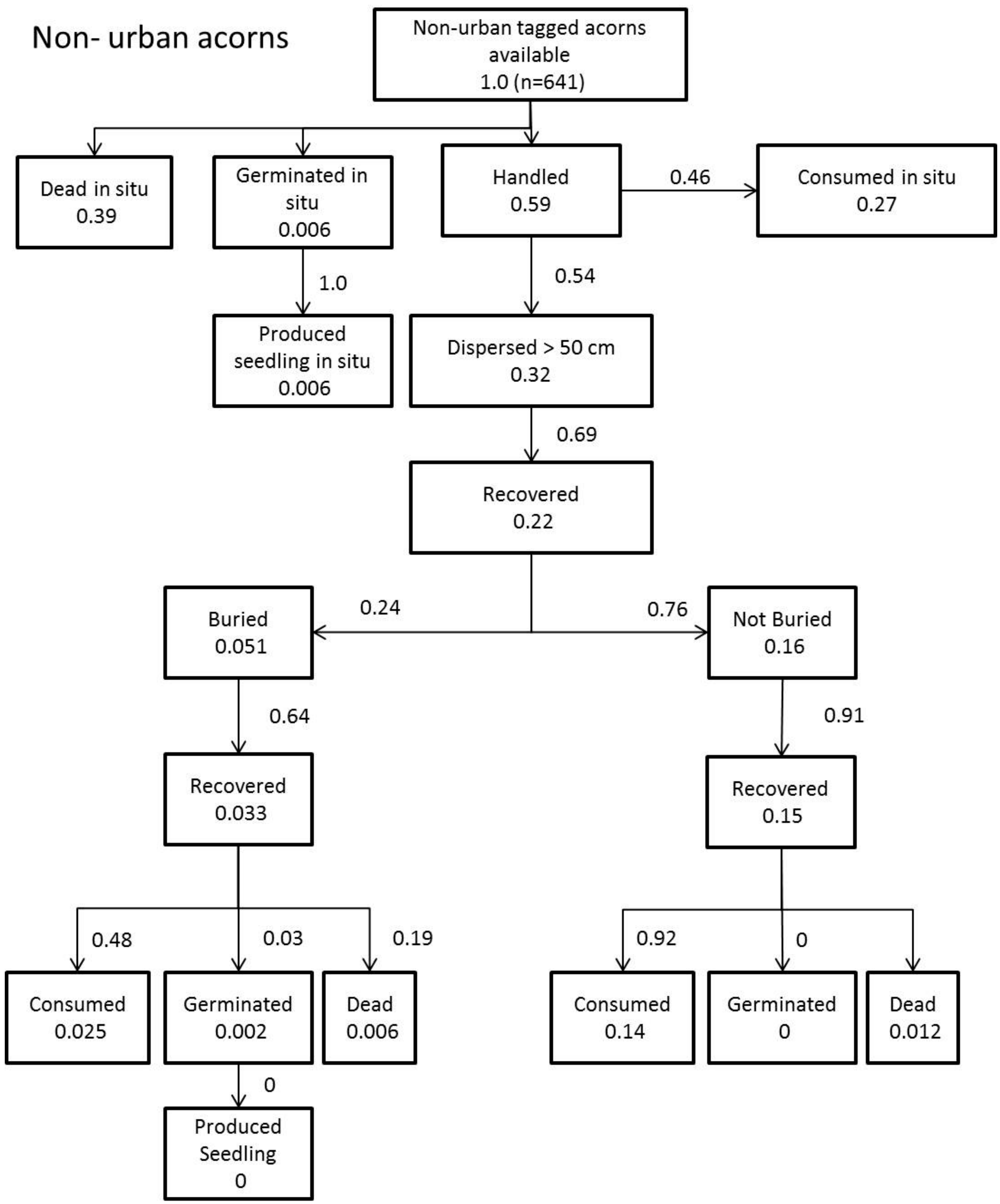

Figure 2.13. Diagram of non-urban acorn fates showing the proportion of acorns moving from one stage to the next (transition probabilities, numbers next to arrows) and the proportion of the initial experimental acorn crop at each stage (values within boxes).

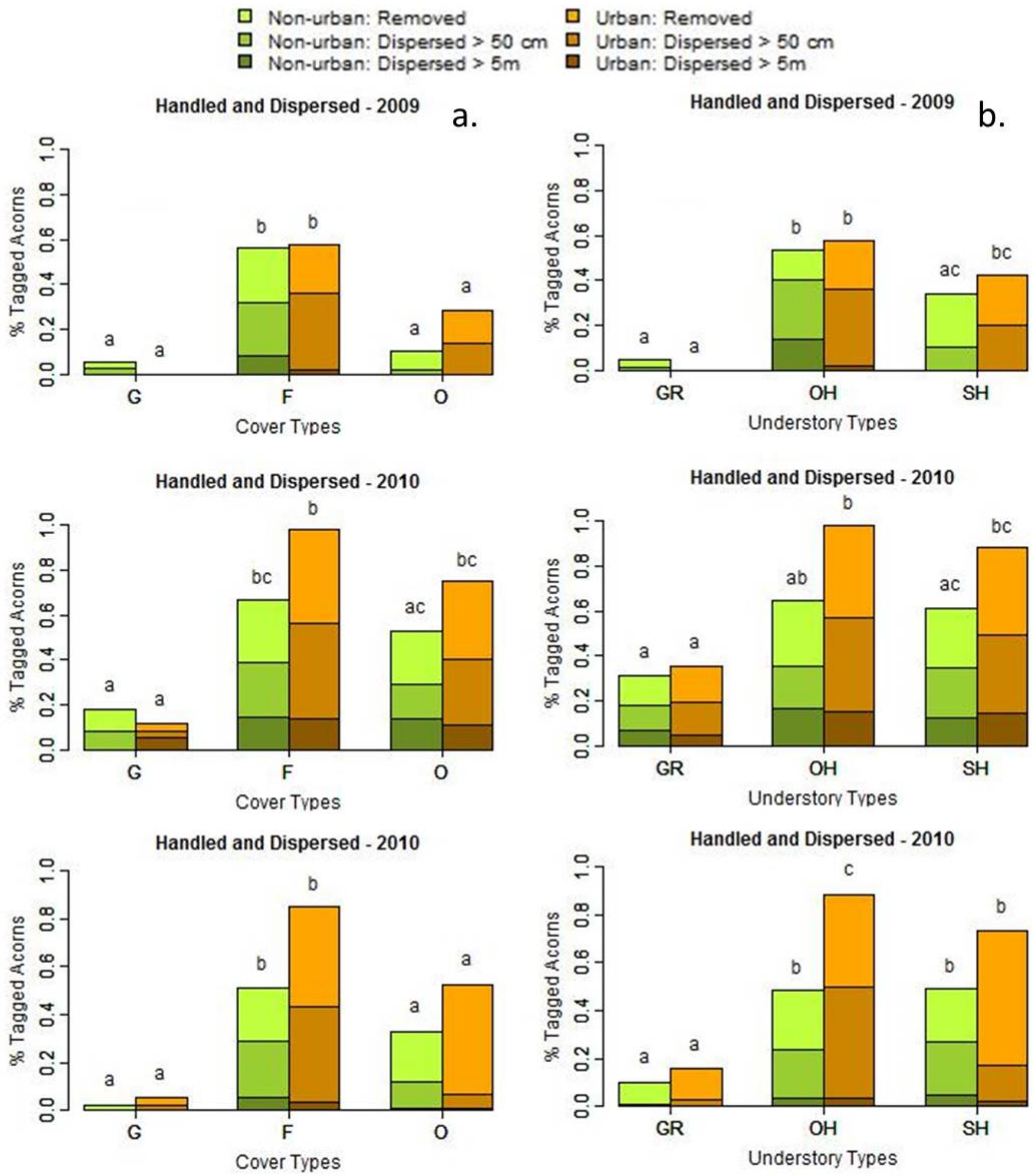

Figure 2.14. Proportion of tagged acorns that were handled, dispersed more than 50 cm, or dispersed more than 5 meters by landscape (urban/non-urban) and year for a) cover type: G = non-forest grassland, F = conifer forest, O = oak, and b) understory type: GR = non-forested grassland, OH = open herb, SH = shrub. Letters indicate significant differences in the number of acorns dispersed more than 50 cm. Bars with the same letter are not significantly different at α < 0.05 after pairwise comparisons. To review significant differences in handling see Figure 2.5. There were not enough observations of acorns dispersed more than 5 meters in each category to test for differences.

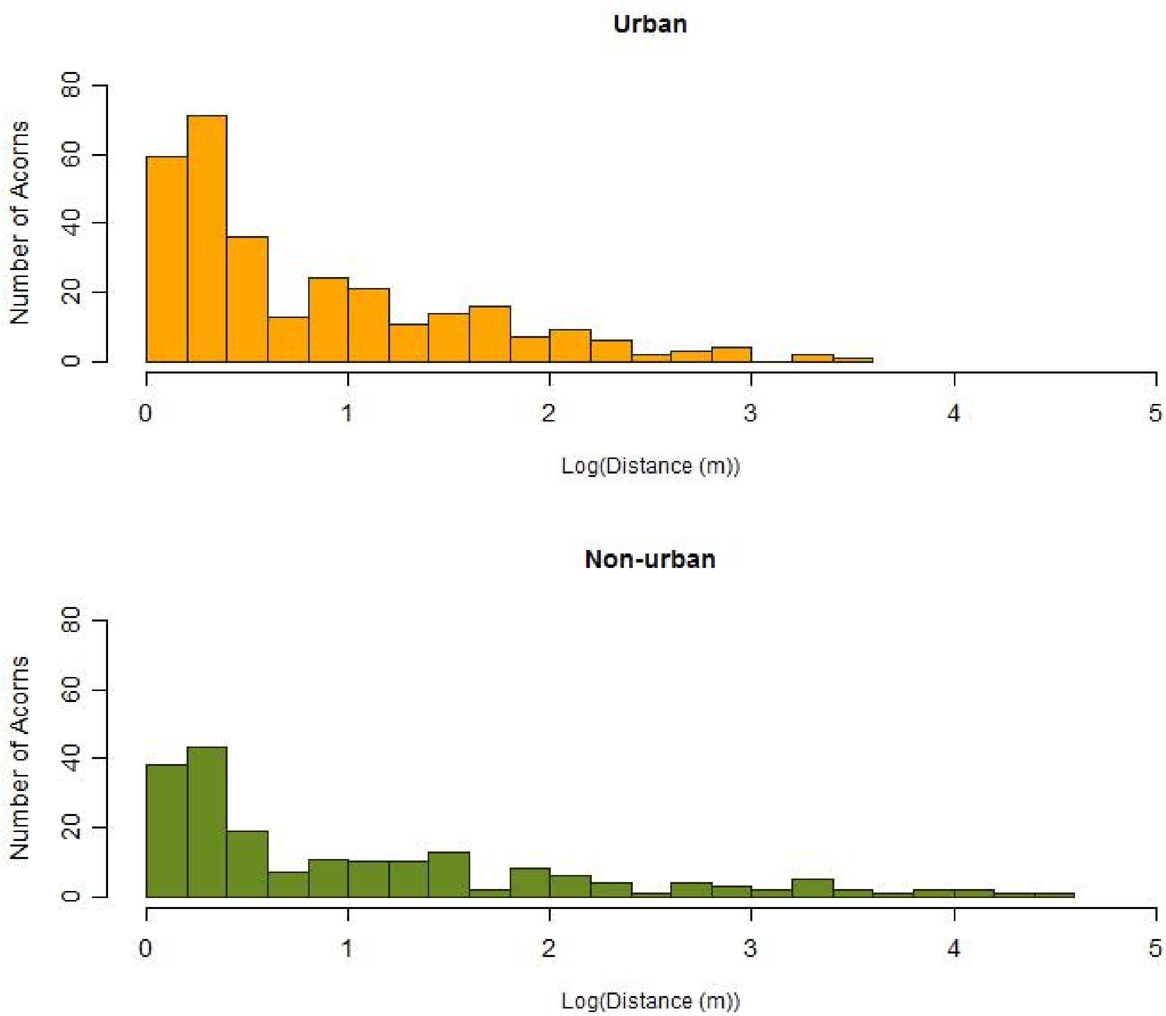

Figure 2.15. Frequency of dispersal distances for urban and non-urban sites. Data shown include all plots and all years.

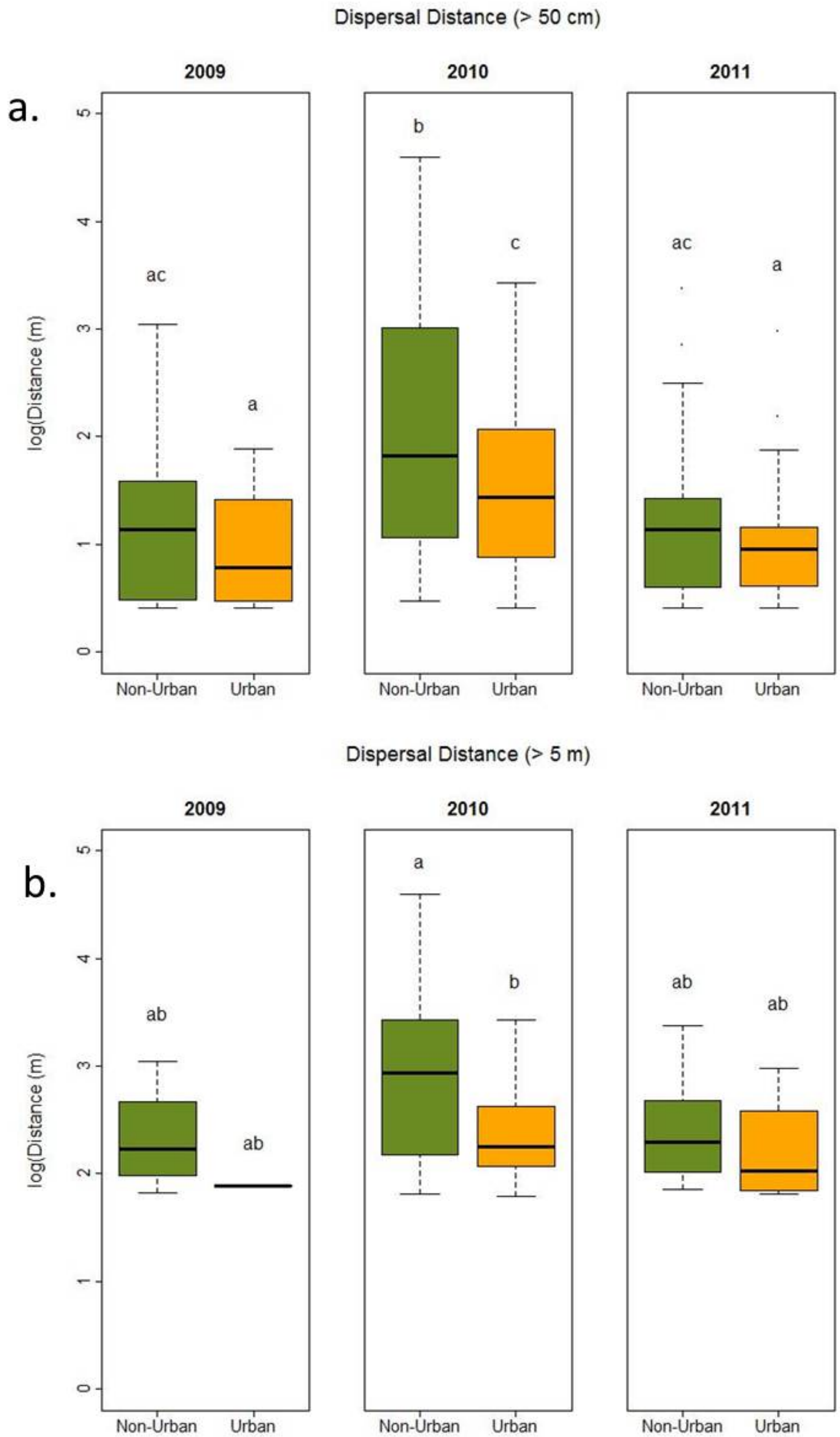

Figure 2.16. Boxplot of dispersal distances for urban and non-urban landscapes. Data are only for a) acorns moved at least 50 cm and b) acorns that moved at least 5 meters. Boxplots with the same letter are not significantly different at $\alpha < 0.05$ after pairwise comparisons.

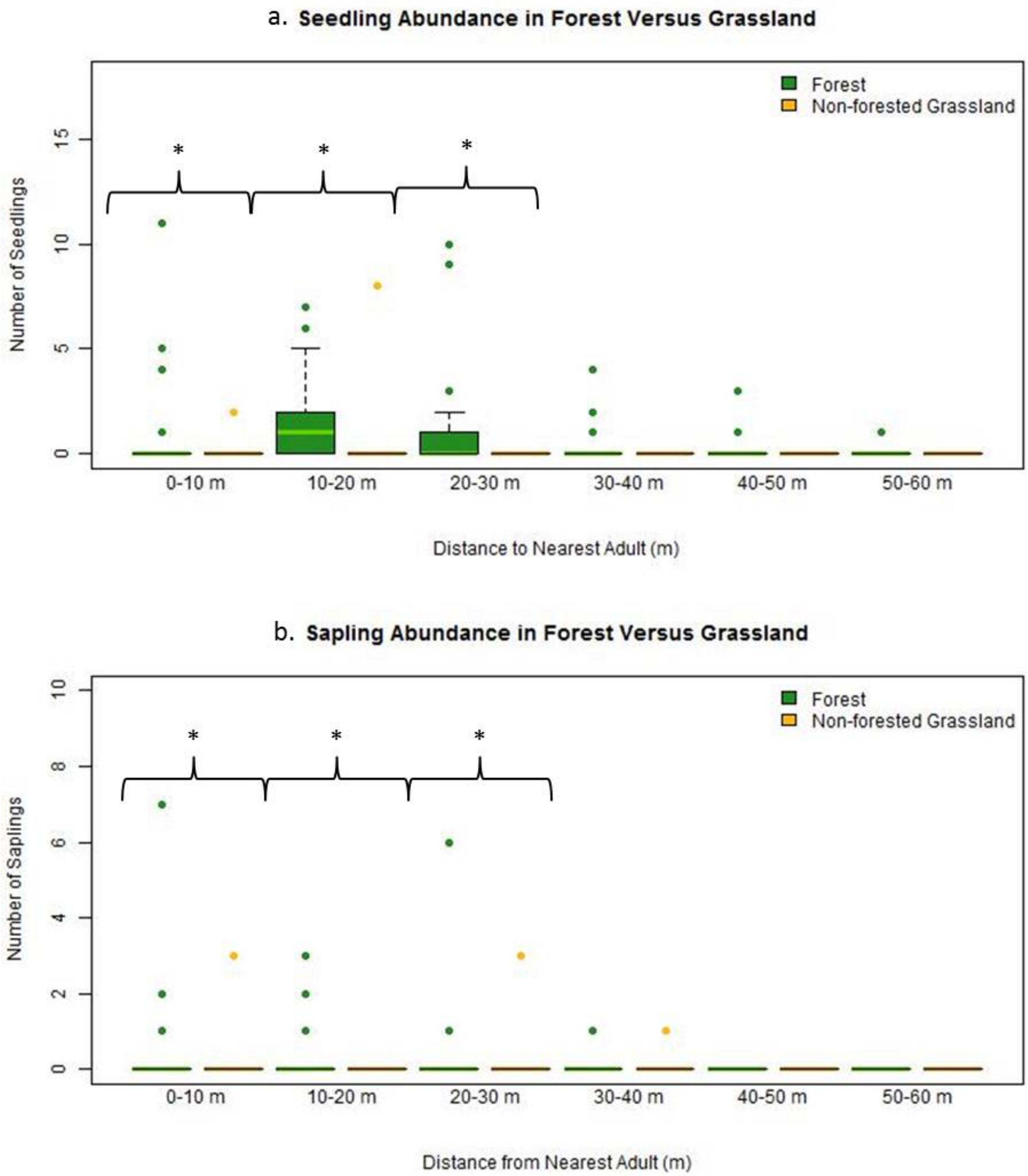

Figure 2.17. Boxplots of a) seedling and b) sapling transect results. Graphs show boxplot summaries of seedling/sapling counts found at increasing distances from the nearest adult oak tree for transects extending into conifer forest and non-forested grassland sites. Bracketed pairs with stars indicate significantly different counts. Both seedlings and saplings were more abundant in forested than in grassland transects up to 30 meters from the nearest adult.

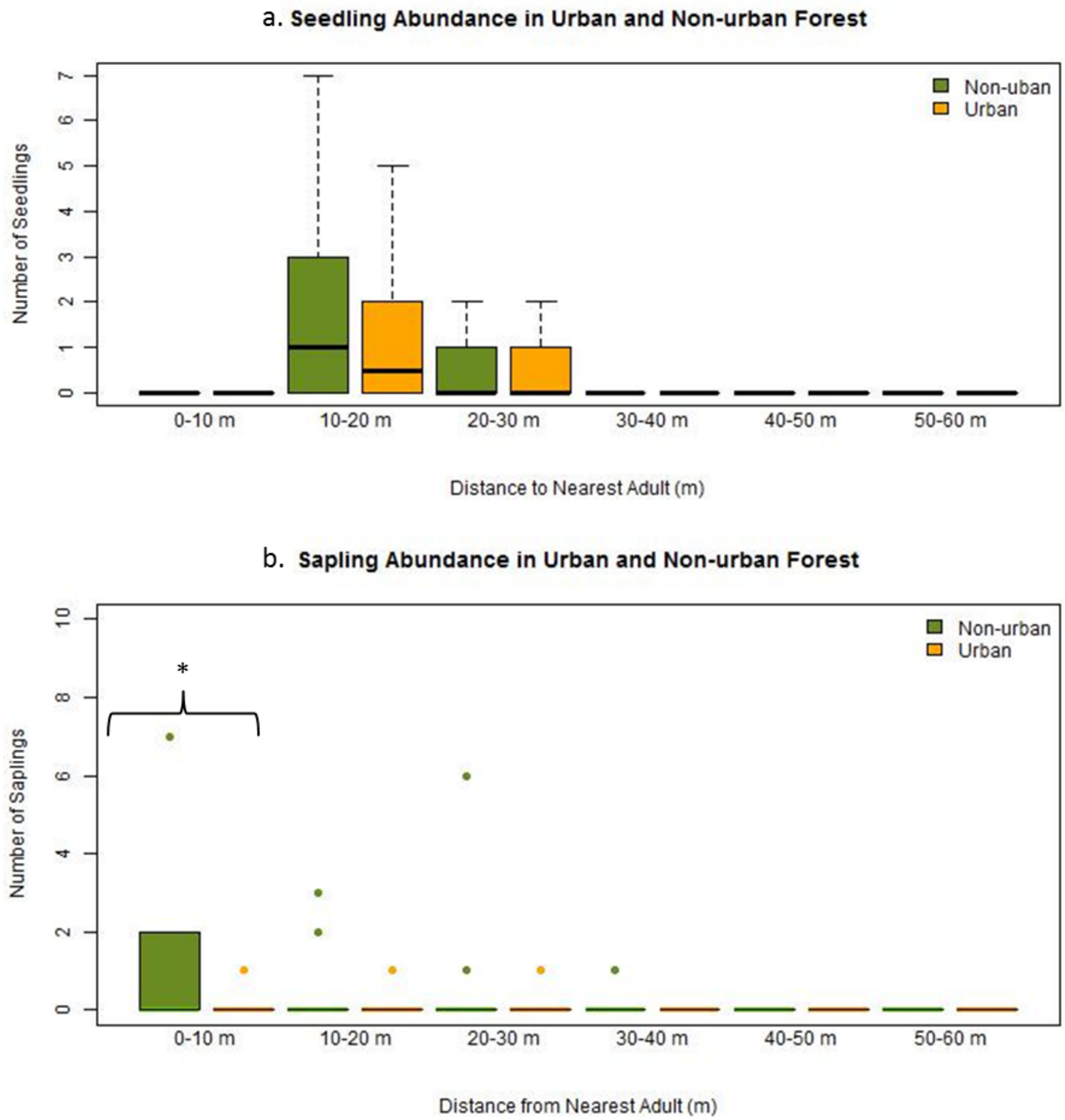

Figure 2.18. Boxplots of a) seedling and b) sapling transect results. Graphs show boxplot summaries of seedling/sapling counts found at increasing distances from the nearest adult oak tree for urban and non-urban transects. Bracketed pairs with stars indicate significantly different counts.

Table 2.1. Description of acorn fates.

Acorn Fate	Acorn type	Fate description
Handled	Un-tagged	Acorn not present within 10 cm of original location
	Tagged	Acorn moved > 10 cm from original location or eaten
Remaining	Both	Any acorn that was not handled is considered "remaining"
Germinated	Both	Radicle has broken through pericarp
Unknown	Un-tagged	Acorn not present within 10 cm of original location
	Tagged	Moved but not recovered
Eaten	Tagged	At a minimum acorn tip including radicle has been removed. If only the tag was recovered, the acorn was assumed to be eaten (Moore et al. 2007)
Dead	Both	Acorn present, desiccated or rotted
Seedling	Both	Oak seedling (either epicotyl or young shoot with leaves) present in original acorn location.
Dispersed	Tagged	Two definitions: either moved > 0.5 or moved > 5 meters from original location

Table 2.2. Summary of Likelihood Ratio Test results for general linear mixed models fit with the binomial distribution.

Dependent	Covariate	df	chi-square	p-value	
Handled	Year	2	**5.9529**	**0.0510**	**.**
n=3730	Urban	1	**7.339**	**0.0067**	**
	Treatment	2	**49.696**	**< 0.0001**	***
	Understory	2	**12.501**	**0.0019**	**
	Canopy Cover Type	2	**28.948**	**< 0.0001**	***
	Plot habitat	4	**111.05**	**< 0.0001**	***
	Canopy Cover %	1	1.3455	0.2461	
Germination	Year	2	**60.067**	**< 0.0001**	***
of remaining acorns	Urban	1	1.7608	0.1845	
n=1835	Treatment	2	**54.176**	**< 0.0001**	***
	Understory	2	1.918	0.3833	
	Canopy Cover Type	2	**28.087**	**< 0.0001**	***
	Plot habitat	4	**35.93**	**< 0.0001**	***
	Canopy Cover %	1	0.4533	0.5008	
Predation	Year	2	**15.742**	**0.0004**	**
of tagged, removed,	Urban	1	**8.2306**	**0.0041**	**
recovered acorns	Canopy Cover	2	2.543	0.2804	
n=561	Understory	2	**12.153**	**0.0023**	**
	Plot habitat	4	**12.72**	**0.0127**	*
	Canopy Cover %	1	0.1303	0.7181	
Seedling Production	Year	2	**17.148**	**0.0002**	**
All acorns	Urban	1	2.0633	0.1509	
n=3730	Treatment	2	**176.66**	**< 0.0001**	***
	Understory	2	**5.3168**	**0.0701**	**.**
	Canopy Cover Type	2	0.6585	0.7195	
	Plot habitat	4	**26.764**	**< 0.0001**	***
	Canopy Cover %	1	2.2753	0.1314	
	Acorn Removal	1	**113.01**	**< 0.0001**	***
Seedling Production	Year	2	**20.35**	**< 0.0001**	***
Remaining acorns	Urban	1	1.371	0.2416	
n=1185	Treatment	2	**162.92**	**< 0.0001**	***
	Understory	2	3.6927	0.1578	
	Canopy Cover Type	2	2.6368	0.2676	
	Plot habitat	4	3.8376	0.1468	
	Canopy Cover %	1	2.097	0.1476	

Seedling Survival	**Year**	**2**	**2.6559**	**0.1032**	
Year 2	Urban	1	2.2424	0.3259	
of Seedlings Produced	Treatment	2	0.3113	0.8559	
in Year 1	Understory	2	3.6108	0.1644	
n=122	Canopy Cover Type	2	5.0798	0.4062	
	Plot habitat	4	**8.2535**	**0.0827**	**.**
	Canopy Cover %	1	0.6946	0.4046	
Seedling Survival	Year	2	n/a	n/a	
Year 3	Urban	1	2.0798	0.1493	
of Seedlings Produced	Treatment	2	n/a	n/a	
in Year 2	Understory	2	**10.842**	**0.0044**	**
n=51	Canopy Cover Type	2	1.3302	0.5142	
	Plot habitat	4	1.9284	0.1649	
	Canopy Cover %	1	0.0478	0.8270	

Table 2.3 Summary of dispersal distances by year and landscape type.

Landscape	Year	n	mean	std.error	min	max	median	kurtosis	skewness
Non-urban	2009	18	3.7	1.1	0.5	19.9	2.1	4.83	2.23
	2010	55	13.9	2.6	0.6	98.1	5.2	5.28	2.17
	2011	39	3.5	0.8	0.5	28.4	2.1	11.42	3.22
	All	112	8.7	1.4	0.5	98.1	3.0	12.50	3.20
Urban	2009	25	2.0	0.3	0.5	5.6	1.2	-0.76	0.79
	2010	90	5.2	0.6	0.5	30.0	3.2	5.88	2.31
	2011	50	2.3	0.4	0.5	18.6	1.6	20.56	4.15
	All	165	3.8	0.4	0.5	30.0	2.1	10.70	3.01
All	2009	43	2.7	0.5	0.5	19.9	1.4	13.56	3.30
	2010	145	8.5	1.1	0.5	98.1	3.8	15.42	3.45
	2011	89	2.8	0.4	0.5	28.4	1.7	18.97	4.01
	All	277	5.8	0.6	0.5	98.1	2.3	27.67	4.53

Table 2.4. Summary of lost acorns by landscape type and year. Acorns lost in spring are in addition to those lost in fall.

	Fall				Spring				Total
	2009		2010	2011	2009		2010	2011	
Landscape	Wire Cut	Missing	Missing	Missing	Wire Cut	Missing	Missing	Missing	
Urban	15	4	22	2	17	8	10	16	94
Non-urban	2	1	24	2	35	4	8	10	86
Total	17	5	46	4	52	12	18	26	180

Table 2.5. Results of Likelihood Ratio Tests for dispersal and caching behavior.

Dependent	Covariate	df	chi-square	p-value	
Dispersed (50 cm min)	Year	2	**15.692**	**0.0004**	**
all tagged acorns with	Urban	1	**3.3043**	**0.0691**	.
at least one distance	Understory	2	3.0976	0.2125	
measure recorded	Canopy Cover Type	2	**55.718**	**< 0.0001**	***
n=1295	Plot habitat	4	**73.979**	**< 0.0001**	***
	Canopy Cover %	1	**16.954**	**< 0.0001**	.
Dispersed (5 m min)	Year	2	**13.297**	**0.0013**	**
all tagged acorns with	Urban	1	0.2586	0.6111	
at least one distance	Understory	2	1.1047	0.5756	
measure recorded	Canopy Cover Type	2	**15.892**	**0.0004**	**
n=1295	Plot habitat	4	**17.158**	**0.0018**	**
	Canopy Cover %	1	1.0006	0.3172	
Buried	Year	2	**13.774**	**0.0010**	**
all tagged acorns with	Urban	1	0.0935	0.7598	
at least one distance	Understory	2	**13.423**	**0.0012**	**
measure recorded	Canopy Cover Type	2	**24.14**	**< 0.0001**	***
n=1295	Plot habitat	4	**25.872**	**< 0.0001**	***
	Canopy Cover %	1	**7.608**	**0.0058**	**
Log(Distance)	Year	2	**15.061**	**0.0005**	**
of acorns dispersed a	Urban	1	**4.3848**	**0.0363**	*
minimum of 50 cm.	Understory	2	1.8969	0.3873	
n=277	Canopy Cover Type	2	0.3355	0.8456	
	Plot habitat	4	2.7602	0.7369	
	Canopy Cover %	1	0.0416	0.8383	
	# of cache sites	1	**10.788**	**0.0010**	**
	Cached in same/different habitat	1	**68.275**	**< 0.0001**	***
Log(Distance)	Year	2	4.0677	0.1308	
of acorns dispersed a	Urban	1	**3.4966**	**0.0615**	.
minimum of 5 m.	Understory	2	0.954	0.6207	
n=75	Canopy Cover Type	2	0.9775	0.6134	
	Plot habitat	4	2.5742	0.6314	
	Canopy Cover %	1	0.13	0.7184	

Table 2.6. Summary of site characteristics and dispersal results.

Site	Urban	Oak Woodland Area (ha)	% Urban 1k	% Forest 1k	Squirrels present	% Removed	# Tagged Acorns	% Tagged Lost	Median Removal Distance (m)	Maximum Dispersal Distance Recorded (m)	% Dispersed > 5 m	Median Dispersal Distance (i.e. acorns moved > 5 m)
12	1	7.41	0.77	0.1	EGS	98%	80	1.30%	1.3	25.2	11.30%	7.9
18	1	1.46	0.74	0.08	EGS	53%	160	1.30%	0.3	8.2	1.30%	7.9
67	1	5.09	0.86	0.07	EGS	64%	120	4.30%	0.7	13	7.50%	8.9
75	1	5.81	0.56	0.07	EGS	63%	80	14.30%	2.05	18.6	11.30%	8.8
90	1	10.89	0.84	0.07	EGS	45%	300	4.20%	0.55	30	2.00%	6.3
189	0	3.29	0.26	0.68	no EGS or WGS (or very low use)	36%	80	6.70%	0.4	2.5	0.00%	n/a
252	0	5.95	0.23	0.69	WGS (intensively used EGS removed in Sp. 2010)	40%	341	1.50%	0.57	98.1	5.90%	13
333	0	6.79	0.2	0.57	EGS and WGS (less intensively used)	41%	140	2.20%	1.6	51.3	5.70%	9.05
398	0	7.3	0.28	0.44	WGS (EGS previously present, removed in Sept 2010)	48%	140	6.10%	0.92	39.2	8.60%	17.8

CHAPTER 3

Uncertainty in Ecological Climate Vulnerability and Adaptation Assessments: Sources and Planning Approaches

INTRODUCTION

Climate change has led to significant changes in species distribution and abundance globally (Chen et al., 2011; Parmesan and Yohe, 2003; Root et al., 2003; Walther et al., 2002), and such changes to biodiversity are expected to accelerate over the next century (Thomas et al., 2004). Assessing the vulnerability of species and ecological systems to climate, or evaluating to what extent and how these resources will respond to climate change, is critical for effective climate adaptation planning (Game et al., 2011; Gillson et al., 2013; Glick et al., 2011; Hannah et al., 2007). However, there are numerous sources of uncertainty in assessing ecological responses to climate change (Littell et al., 2011). Uncertainty can result from: 1) variation in projected levels of greenhouse gas emissions and how climate will respond to emissions (IPCC, 2007a); 2) how ecological systems will respond to climate changes at a broad scale (Littell et al., 2011; Millar et al., 2007); 3) how climate change will influence ecological community structure and interactions at fine scales (Gilman et al., 2010), and 4) how non-climate stressors such as land-cover change will change over time and interact with climate change (Carroll, 2007).

There are two broad approaches to addressing uncertainty in ecological planning. First, uncertainty may be reduced, or at least bounded, by integrating a variety of climate vulnerability information resources (Dawson et al., 2011). For example, comparing projected changes using multiple climate scenarios and modeling approaches (Littell et al., 2011). However, uncertainty as to how ecological systems will respond to climate change can never be eliminated completely

(Millar et al., 2007). Scenario-based planning is one promising strategy for addressing irreducible uncertainty and facilitating the identification of flexible and robust management strategies (Gillson et al., 2013; Peterson et al., 2003). In this chapter, I explore the application of these two approaches to addressing uncertainty in the context of climate vulnerability assessments and adaptation planning. The approach outline here is specifically tailored to planning for a targeted species or ecological system within a defined management landscape such as an ecoregion or existing protected area.

A variety of information resources can inform ecological climate vulnerability assessments including, but not limited to, climate and ecological response models, observational and experimental data, and natural history knowledge of species traits and ecology (Dawson et al., 2011; Rowland et al., 2011). Integrating these multiple resources is important because each provides unique insight into different aspects of climate vulnerability but is incomplete on its own (Dawson et al., 2011; Guisan et al., 2013; Kearney and Porter, 2009; Rowland et al., 2011; Wilsey et al., 2013). Given the uncertainty and limitations associated with individual modeling and assessment approaches, relying on only one information source to project future ecological conditions increases the chances that managers will miss important dynamics driving ecological change and leave them unprepared for surprises (Millar et al., 2007).

In the case of climate change projections, researchers generally consider an outcome more likely if it is projected by multiple independent models (Hansen et al., 2001; Littell et al., 2011). Similarly, comparing ecological response projections based on a variety of modeling approaches (Morin and Thuiller, 2009) or climate scenarios (Rehfeldt et al., 2012) can provide greater confidence in future outcomes if projections agree (Pearson and Dawson, 2003). In addition, comparing model projections with logical resource responses based on observational and experimental data or general natural history knowledge can provide important insights into model limitations. In particular, natural history knowledge can identify processes that operate at spatial or temporal scales too fine to be captured in formal climate or ecological response models.

While agreement among different resource response projections can build confidence in a particular future outcome, there is good reason to believe that such agreement will be elusive. As climate models have proliferated and advanced in complexity, agreement among climate projections has gone down (Maslin and Austin, 2012). When using quantitative ecological response models, projections can vary depending on: 1) the climate scenario used; 2) whether the model is statistical (i.e. based on correlative, statistical relationships between species distribution and observed climate conditions) or process-based (i.e. based on known ecological or physical mechanistic relationships linking climate to species or ecological system response) (Hijmans and Graham, 2006; Morin and Thuiller, 2009) ; and 3) the specific model used (e.g. General Linear Models, Maximum Entropy, or Random Forest) (Fordham et al., 2012; Lawler et al., 2006). Disagreement among projections highlights uncertainty and can therefore identify areas for further research (Pearson and Dawson, 2003). In addition, comparing results from multiple independent assessments, conducted using a variety of methods, can help create more robust climate adaptation plans (Morin and Thuiller, 2009). This is because using results from a variety of sources is likely to identify a wide range of different potential future conditions and help keep managers from focusing too heavily on one most likely outcome.

Despite the theoretical importance of using multiple information resources for assessing climate vulnerability, the majority of adaptation case studies have relied on general characterization of climate impacts and expert opinion alone (e.g. Cross et al., 2012; Glick et al., 2011; Poiani et al., 2011). In the cases where ecological response models have been applied, analyses have most often relied on a single modeling approach, mostly climatic niche models (also referred to as bioclimatic envelope models or species distribution models) (Dawson et al., 2011). For example, numerous studies have illustrated how niche models can be used to project species turnover in specific protected or management areas (e.g. Araújo et al., 2004; Guisan et al., 2013; Hole et al., 2011; Midgley et al., 2003). There are fewer examples of studies using process-based models for adaptation planning (Morin and Thuiller, 2009). Although Glick et al. (2008) used a process-based model to project changes in marsh habitat in the Chesapeake Bay due to sea level rise, assess climate vulnerability, and identify adaptation actions. Finally, there are examples of adaptation plans that incorporate the full suite of climate vulnerability information (e.g. Bachelet et al., 2011; Halofsky et al., 2011). However, in these cases, variability in projected ecological responses is not explicitly addressed as uncertainty and not directly linked to developing adaptation strategies.

Effective adaptation planning can be initiated using expert knowledge alone (Cross et al., 2012), as managers in many regions do not have access to projections from quantitative ecological response models. However, as quantitative models become more available, managers need practical examples of how to integrate and apply resulting projections to landscape management. In the Pacific Northwest (PNW), an increasing number of information resources for assessing climate vulnerability have recently been developed. In addition to basic natural history and expert knowledge, climate vulnerability information resources in this region include, downscaled (~ 1-kilometer) projections of climate change variables (Shafer and Bartlein, 2011), statistical climatic niche models (e.g. Case and Lawler, 2012; Rehfeldt et al., 2012), dynamic global vegetation models (e.g. Rogers et al., 2011), and a species sensitivity database (Case, 2013). In this chapter, I: 1) review the variety of information resources available for conducting climate vulnerability assessments and identify their strengths and weaknesses from a vulnerability assessment perspective; 2) provide a practical checklist of questions to help managers integrate diverse, and potentially conflicting, information resources into ecological climate vulnerability assessments; 3) outline an approach for developing "resource response" scenarios to incorporate irreducible uncertainty directly into adaptation planning; and 4) take advantage of the variety of information resources available for the PNW to evaluate climate vulnerability of Oregon white oak (*Quercus garryana*) in the Willamette Valley ecoregion of Oregon as a case study.

Overview of the Adaptation Planning Process

Understanding potential climate impacts is a necessary step towards identifying adaptation actions (Snover et al., 2007), and so, vulnerability assessments have an important role to play in informing adaptation planning (Figure 3.1). Adaptation planning begins with the definition of a focal issue or management objective (Cross et al., 2012). Having a clearly defined ecological management objective, within a bounded geographic region, improves feasibility by narrowing the scope of the initial analysis (Cross et al., 2012; Rowland et al., 2011). The approach presented is designed to facilitate vulnerability assessment and adaptation planning for species, habitats, or ecological systems. I refer to these as conservation or management "targets." In addition, the approach is focused on planning for a defined geographic landscape, such an ecoregion or sub-landscape within an ecoregion.

The next step is to develop a conceptual model of the most important factors influencing the management target. Narrowing down the number of factors most critical to the system's behavior helps to focus the vulnerability assessment. For example, the conceptual model can identify key climate variables, ecological processes, non-climate stressors, or interacting species that are particularly relevant to the target. Identifying these processes and drivers helps with selecting appropriate and relevant ecological response models and guiding literature reviews into the natural history and ecology of the system.

Focusing on a defined geographic region is useful because there is likely to be less variability in both climate changes and ecological responses within a defined area, such as an ecoregion or landscape, which only spans a few hundreds of kilometers. Therefore, narrowing the geographic extent may reduce some of the variability in expected change. In addition, management strategies may be more realistic and informative if they are targeted to a specific geographic region because they can then account for specific contextual factors such as socio-economic conditions. Focusing on smaller spatial extents (i.e. less than a few hundred square kilometers) is challenging because even downscaled climate and ecological response projections are not available at resolutions finer than 1-kilometer.

Finally, while focusing on a particular region is useful, viewing projected changes across the species' or system's full geographic range can help identify general patterns (i.e. shifts poleward or up in elevation) and provide context for projected changes (or stability) in the focal region. Specifically, evaluating vulnerability at this broader extent can provide insight into the role a specific geographic region can play in the target's conservation. For example, if a species is stable within the geographic region of interest, but losing significant habitat outside that region, the focal region may be an important climate refuge for that target.

Information Resources: Strengths and Limitations

Vulnerability assessments evaluate the degree of climate change impact that individual species or systems are expected to experience and, importantly, why (Glick et al., 2011). Climate vulnerability is defined as the interaction between exposure, sensitivity, and adaptive capacity (IPCC, 2007b). Exposure measures factors extrinsic to the species or system including the degree and rate of climate change and related impacts in a given location. Sensitivity is the degree to which a species' or system's intrinsic survival, reproduction, performance, etc. depends on climate conditions. Adaptive capacity is the ability of a species or system to adapt to changing climate conditions, for example through migration to new locations or evolution (Glick et al., 2011). Breaking down climate impacts into these three components greatly facilitates identifying adaptation actions as strategies can target the source of vulnerability directly (Glick et al., 2011).

Exposure can be assessed using climate projections from Global Circulation Models (GCMs) and measured as the degree and rate of change in climatic variables of interest. Evaluating exposure due to associated climate impacts, such as changes to fire regime, habitat suitability, or disease is more challenging and requires the use of targeted ecological response models. These response models can range from formal quantitative, mechanistic or statistical models, or informal conceptual models, depending on availability. Sensitivity and adaptive capacity can each be addressed using a range of information sources including natural history, paleoclimatic data, as well as ecological response models (Dawson et al., 2011).

Here I review three main types of climate vulnerability information: 1) statistical climatic niche models, 2) mechanistic or process-based models, and 3) trait-based sensitivity assessments based on natural history and expert opinion. Much has been written on the strengths and limitations of different modeling approaches (Araújo et al., 2005; Hampe, 2004; Kearney and

Porter, 2009; Littell et al., 2011; Pearson and Dawson, 2003; Rowland et al., 2011), and so I provide only a brief summary here. The objective of this review is to show how each information resource can be used individually and collectively to assess climate vulnerability.

Statistical Climatic Niche Models

Climatic niche models provide spatially-explicit projections of how changing climate conditions may influence the geographic range of a species or ecological system (i.e. habitat type, biome or vegetation association). These models assume that the climate conditions found within a species' current range provides a reasonable estimate of climate conditions tolerated by that species. Modelers use a statistical approach to define the climate conditions that are correlated with current species range boundaries and then use projections of future climate conditions to identify where, on the landscape, a species' "climate envelope" is likely to be in the future (Pearson and Dawson, 2003). From a vulnerability perspective, these models integrate sensitivity and exposure. They evaluate one measure of sensitivity by defining the observed range of climate conditions currently tolerated by the species or system. This sensitivity is then linked to exposure by projecting the target's new range based on projected climate changes. Importantly, these models do not generally include factors affecting adaptive capacity such as dispersal ability, landscape structure, or evolutionary capacity.

Climatic niche models are comparatively fast to implement and do not require detailed ecological knowledge of the mechanisms linking climate and species' distribution (Rehfeldt et al., 2006). Consequently, these models can be applied to a large number of species (Lawler et al., 2006). Compared to more complex mechanistic models which project changes based on interactions between a wide range of factors, climatic niche models are more straightforward to interpret because they are usually based solely on the relationship between climate and species' range. Finally, overall, climatic niche models have been successful in predicting observed current distributions (Beerling et al., 1995; Pearson et al., 2002), range changes observed for many species over the last century (Araújo et al., 2005; Green et al., 2008), and observed shifts due to recent climate changes (Walther et al., 2005).

However, climatic niche models have numerous limitations and their validity has been the focus of significant debate in recent years (Hampe, 2004; Pearson and Dawson, 2003). These models do not account for physiological, ecological and evolutionary factors, such as dispersal, competition, or the ability to adapt *in situ*, that limit a species' distribution and abundance. Based on these limitations, a valid interpretation of these models is that they project where the climate conditions currently tolerated by the species or system are projected to be in the future, but do not predict future species' distributions (Dawson et al., 2011; Pearson and Dawson, 2003; Rehfeldt et al., 2012). In addition, these models are best applied at broad (i.e. continental) spatial scales, where the effects of fine-scaled topography and biological interactions play a smaller role (Pearson and Dawson, 2003).

Overall, climatic niche models provide a sense of whether the climate is projected to become more or less similar to the current climate occupied by a given species in a given region in the future. This information can give managers a sense of whether, based on climate factors alone, habitat conditions are expected to improve, degrade or remain stable. Climatic niche model results should not be used in isolation to determine management actions. At a minimum, climatic niche model results need to be viewed in the context of the ecology and natural history of the focal species or system within the management region. Ideally, climatic niche projections can be compared with mechanistic model results to provide further insight into how ecological processes may interact with climate changes (Morin and Thuiller, 2009). The following list of caveats is important for managers to consider when selecting and applying climatic niche projections:

- Biotic interactions such as competition, predation, or the presence/absence of co-evolved species can limit a species' ability to occupy climatically suitable areas. Where this is the case, climatic niche models will over-estimate the amount of area that is climatically suitable for a given species (Davis et al., 1998; Morin and Thuiller, 2009).
- Human activities may have extirpated a species from large portions of their range. In this case, climatic niche models should be based on the historical rather than observed range (Lawler, personal communication).
- Areas currently occupied by a species may be sinks that are supported by dispersal. These areas could not sustain a population in the absence of dispersal (Davis et al., 1998). If this is the case, climatic niche models may identify areas as climatically suitable that are in fact marginal.
- Errors in current distribution maps will lead to errors in projections of expansion and contraction. Check with local experts familiar with the distribution of a species in the focal region to assess whether projected changes are logical given current known distribution (Author's personal observation).
- Dispersal in the absence of active intervention will likely limit the ability of a species to colonize currently unoccupied areas that become climatically suitable in the future (Morin and Thuiller, 2009; Schloss et al., 2012).

- Species may be able to persist in areas that become climatically unsuitable if they can 1) genetically or behaviorally adapt to new climatic conditions or 2) find climate refuges, or fine-scaled locations that remain climatically suitable within a given region despite broad-scale changes (i.e. moving from south to north facing slopes). Examples of persistence *in situ* during the Quaternary climate change suggest that adaptation and refuges can help some species (Davis and Shaw, 2001). A comparison of range shifts modeled using climatic niche and mechanistic models found that the niche models projected more extreme shifts (greater contraction and expansion) than the mechanistic models for 10 out of 15 tree species assessed. The authors suggest that this discrepancy is due to the inclusion of phenotypic plasticity and local adaptation in the mechanistic models (Morin and Thuiller, 2009). However, the pace of climate change projected over the next century is significantly more rapid that that observed during the Quaternary, suggesting that *in situ* adaptation and persistence should not be assumed (Davis and Shaw, 2001).
- While there is currently strong data supporting range expansions in response to climate change, there are fewer empirical examples of contractions (Dawson et al., 2011; Walther et al., 2002, 2005), although some do exist (Moritz et al., 2008). Ettinger et al. (2011) found evidence that climate controls tree growth at its upper elevation range on Mt. Rainier, but that biotic controls are more likely at low elevation limits. If this finding is generalizeable, then climatic niche models make be more accurate in projecting range expansions than contractions. Alternatively, documenting expansions may be more feasible than contractions, which may take generations to become apparent (Jackson and Sax, 2010).

Mechanistic Models

Mechanistic, or process-based, models address many of the limitations of climatic niche models. Specifically, these models capture interactions and feedbacks among ecological processes such as wildfire, CO_2 fertilization, predation, competition, disease, and water use efficiency (Bachelet et al., 2001; Kearney and Porter, 2009; Sitch, 2000). Dynamic Global Vegetation Models (DGVMs) are the most commonly used mechanistic models (e.g. MC1 - Daly et al., 2000; the LPJ - Lund-Potsdam-Jena - Sitch et al., 2003). However, mechanistic species distribution models linking climate, physiology and reproduction are also starting to be developed (Buckley et al., 2010; Kearney and Porter, 2009) as well as spatially-explicit population models that incorporate climate change (Carroll, 2007). DGVMs simulate the distributions and productivity of broad vegetation or plant functional types (PFTs), such as grass or evergreen needle-leaved trees, using a variety of mechanistic processes (e.g., photosynthesis, resource competition, population dynamics, etc.). Mechanistic models can theoretically incorporate all three elements of vulnerability. They address exposure by incorporating climate change projections. By including biotic processes, these models can provide insight into both inherent sensitivity and adaptive capacity to climate change (Dawson et al., 2011).

At a most basic level, mechanistic or process-based models can be used to project broad-scale species distribution changes analogous to statistical climatic niche models. Mechanistic models can be used to test hypotheses about the underlying causal factors driving projected range shifts and the effectiveness of proposed management actions. For example, mechanistic models have been used to test how dispersal ability affects adaptive capacity in fragmented landscapes (Wilson et al., 2009). Also, because mechanistic models are based on fundamental, biophysical relationships, they are valid to apply to novel situations such as no-analog climate conditions

(Kearney and Porter, 2009). Because they include biotic processes, mechanistic models can project changes at finer scales than climatic niche models (Morin and Lechowicz, 2008). Lastly, mechanistic models are particularly useful in evaluating the net impact of competing processes. For example, these models can estimate under what conditions a decrease in precipitation, which should favor grassland, will be a more important driver than an increase in CO_2 concentrations, which should favor tree growth (Rogers et al., 2011).

While these models incorporate ecological processes, and therefore theoretically model ecosystem dynamics more realistically, mechanistic models still have significant limitations. The most important is our limited empirical understanding of the physiological and ecological responses of plants and animals to climate changes (Hijmans and Graham, 2006). For example, the relationship between increases in CO_2 concentrations and water-use efficiency is based on a relatively small number of studies on specific plant species which may not apply to larger scales or diverse plant communities (Rehfeldt et al., 2012). In general, mechanistic models are complex, difficult to parameterize and validate, and a lack of data limits their application to particular species and regions (Kearney and Porter, 2009; Pearson and Dawson, 2003). The mechanistic modeling process is less accessible to non-expert audiences. Finally, these models are simply not available for many regions and species at the present time.

Trait-based Sensitivity and Vulnerability Approaches

Quantitative models are attractive for climate vulnerability assessment because they can provide spatially-explicit projections of how a species' or ecological system's distribution will change in the future. However, due to the significant uncertainties and limitations of modeling approaches outlined above, many managers are, rightly, uncomfortable relying solely on the projections of quantitative models for decision-making. Consequently, conceptual assessments of vulnerability can be conducted based on current understanding of the target's natural history and ecology and such assessments provide an important complement to quantitative modeling.

A number of formal frameworks for defining sensitivity and adaptive capacity to climate change based on inherent species or system characteristics are available (Berg et al., 2010; Case, 2013; Glick et al., 2011; Huey et al., 2012; Rowland et al., 2011; Young et al., 2012). These approaches involve qualitatively evaluating traits that theoretically will influence the degree of impact climate change has on a species as well as their ability to adapt to those changes. Examples of such traits include physiology, dispersal ability, dependence on a sensitive habitat, and reproductive rate (Berg et al., 2010; Case, 2013; Huey et al., 2012).

In some cases, software is available that guides users through the sensitivity assessment using a survey questionnaire and uses the results to calculate a sensitivity index for the species or system (e.g. Young et al. 2011; Case, 2013). For example, the Climate Sensitivity Database (Case, 2013) walks users through a series of questions relating to the species' ecology including: degree of ecological specialization, physiological sensitivities to climate, reproductive strategies, reliance on climate sensitive habitats, dispersal ability, response to disturbance regimes, sensitivity to non-climate threats, etc. Within each category, species experts assign each species/system a numeric ranking (1 being the least sensitive and 7 being the most sensitive to climate change) for each of these life history categories based on best available science. Additional specific questions are included for each category to highlight particular life history characteristics that drive climate change sensitivity. For example, the average length of time to reproductive maturity could influence a species ability to adapt to changing conditions. In addition, experts also assign a confidence ranking to each sensitivity score that indicates their level of confidence in the information provided in each category.

These databases provide important natural history information that can be used to complement, or possibly even parameterize, the modeling approaches listed above. The information does not rely on climate projections or assumptions about future climate conditions. Instead, it highlights known or logically assumed climate sensitivities. Although each species or system may be given a score, the components making up the index are all individually available in the database making the information transparent. The index is easily interpretable unlike the models above which require some expertise to understand. Online databases can be easily updated as new research is generated and the data are publically available.

However, trait-based sensitivity databases and assessments are, of course, also limited by our lack of knowledge of individual species and systems. Published reports should be used when available, but often are not available and expert judgment must be used instead. However, assumptions based on expert judgment can be flawed (Epps et al., 2005). Often, the assessment of species' sensitivity is based on assumed but not tested relationships and usually, the information is not spatially explicit. It is particularly difficult to estimate the net effect of conflicting processes without using a quantitative model. Finally, literature reviews and data gathering necessary to develop the assessment is time consuming even for experts with detailed knowledge of the target species or system. Database formats that make these assessments available to the public are critical to leverage the effort required to complete each assessment. Online databases that allow entries to be updated can help keep information current, but finding the resources for this kind of maintenance is a constant challenge.

A VULNERABILITY ASSESSMENT CHECKLIST

In the following section, I present a checklist of questions for assessing climate vulnerability of species or habitats in a selected focal region. The overarching goal is to compare, qualitatively and when possible quantitatively, how climate change will alter the ecological suitability of the focal region for the target species or habitat. Projected changes are measured against our understanding of present or recent historical conditions. Although present condition is not necessarily the desired state, it is provides a baseline against which to compare future changes. When information is available, it is also important to compare projected changes to long-term historical conditions.

Including as many information sources on climate vulnerability as possible is valuable, depending on availability and relevance, because each source provides unique information and is incomplete on its own (Dawson et al., 2011; Littell et al., 2011; Morin and Thuiller, 2009; Rowland et al., 2011). The vulnerability assessment can be organized into three main phases: 1) assessing direct climate impacts, or climate suitability, based on physical limitations and climatic niche models; 2) assessing indirect climate impacts (e.g. to what extent climate change alters disturbance regimes such as fire or flooding, and ecological community interactions such as competition, predator-prey relationships, or mutualisms) using natural history and mechanistic models; and 3) evaluating non-climatic, interacting threats. Each phase adds additional complexity, and consequently uncertainty, to the evaluation as progressively more factors are included. Whenever possible, classifying impacts as affecting exposure, sensitivity, or adaptive capacity can help clarify the assessment and facilitate the identification of management strategies later on.

Evaluating Direct Climate Impacts

The goal of this phase of the assessment is to focus on how climate changes, in the absence of interacting factors, will affect the target's function and/or distribution. Within the vulnerability framework, assessing climatic suitability focuses on the interaction between exposure and sensitivity with an emphasis on climatic variables that directly impact the species' or system's viability. Complexity is simplified, at least temporarily, by focusing solely on uncertainty in how climate will change and how the management target will respond to changes in climate variables. Managers can evaluate direct impacts by identifying key climate variables that drive important aspects of a species' biology or system behavior (i.e. sensitivity), quantifying the amount of change expected in the focal area (i.e. exposure) and then either qualitatively or quantitatively estimating expected impact (e.g. Mantua et al., 2010).

Climatic niche models are particularly useful for evaluating climate suitability as these models account for changes in multiple climate variables simultaneously. When available, mechanistic species distribution models can incorporate known physiological relationships between climate and the focal species' biology (i.e. reproduction, survival etc.) rather than relying observed correlation between climate and the species' current range (Kearney and Porter, 2009). Although climate is only one of many factors driving ecological distribution, for many species, it is one of the most significant (Chen et al., 2011; Davis and Shaw, 2001; Jacobson Jr et al., 1987; Parmesan, 2006; Walther et al., 2002). In addition, most biotic factors further constrain a species' distribution within its climatically suitable range (Davis et al., 1998). Consequently, identifying areas of climatic suitability provides an important first cut in the process of identifying where a species will have the best chance of persisting and/or establishing in the future.

Importantly, climatic niche models do not capture fine-scaled climate changes such as heat waves or storm events that may have a serious impact on the management target. The impacts of these changes can be evaluated qualitatively and potentially included in scenarios if they are deemed important and uncertain enough.

I developed the following checklist of questions to assist managers in assessing direct climate impacts on species and ecological systems:

- Which climate variables, if any, are known to constrain the abundance and distribution of the conservation target (Sensitivity)? Examples include temperature dependent sex ratios or optimal temperature ranges for ectotherms.
    - Review natural history knowledge from the climate sensitivity database, the literature and of local experts to identify climate variables that may constrain the target.
    - If available, identify which variables are most important to climatic niche models for the target: do these make ecological sense?
- How are these key climate variables projected to change with respect to the physiological needs of the species or system (Exposure)?
    - Remain the same
    - Improve
    - Degrade
- Using results from climatic niche models, if available, classify distributional changes to the species/system both throughout its range and in the focal region as:
    - Stable

    - Expanding
    - Contracting
    - Uncertain (no clear pattern)
- What aspects of climate are not addressed in current models, but could influence management of the conservation target? Examples include:
    - Increased potential for storms (precipitation and wind events)
    - Changes in the intensity and occurrence of extreme events such as heat waves or high precipitation events
    - Changes to hydrology (flow rates and timing, water temps, increased likelihood of rain on snow events)

Evaluating Indirect Climate Impacts

Within the climatically suitable range, ecological factors such as disturbance, competition, predation, or the absence of an important pollinator or food resource may further constrain a species' distribution. When climate change affects these factors there is an indirect (though not necessarily small) impact on the management objective. Assessing indirect effects can increase the complexity of the analysis substantially as uncertainty stems not only from climate changes themselves but how these changes will impact intermediate factors and how the intermediate factor interacts with the management target. In this phase of the assessment, models, observational and experimental data can all be applied to evaluate climate impacts on interacting factors and subsequently the management objective.

Maintaining appropriate habitat or general vegetation type is fundamental for a species or system to persist. Habitats can be qualitatively assessed for sensitivity (Case, 2013). For example, low lying coastal regions are sensitive to sea level rise and ephemeral wetlands are highly sensitive to small changes in precipitation. However, for at least some regions both correlative and mechanistic models of vegetation change may be available (e.g. Rehfeldt et al., 2012; Rogers et al., 2011) and can be cross-referenced with climatic niche projections for the management target itself. Discrepancies between model projections can be informative. For example, climatic niche models may suggest that an area will remain climatically stable for a grassland species but mechanistic model results suggest the region will convert from grassland to forest. This apparent discrepancy can highlight factors outside of climate suitability, such as CO_2 fertilization, that may be important to habitat dynamics.

Natural history knowledge and sensitivity assessments provide additional information regarding how climate change may affect biotic factors that affect the target species' range and population dynamics. Examples of biotic factors include important prey or forage species, predators or herbivores, insect or disease pests, and pollinators or seed dispersers. When available, range shift models can provide insight into how climatic suitability may change for these interacting species. Gilman et al. (2010) provide a framework for assessing the effect of species interactions on responses to climate change. The framework recommends identifying a relatively small unit (2-6 species) of closely interacting species, referred to as community modules. Simplifying the system to a smaller core of interacting species can help clarify potential interspecific dynamics under climate changes.

I developed the following checklist of questions to help managers assess indirect climate impacts and vulnerabilities of the focal species or system:

- Evaluate projected changes to associated habitat, biome, or vegetation types:

- Qualitatively, how sensitive is the habitat to climate change? Sensitivity assessment frameworks are available to assist with this effort (Case, 2013)
- If vegetation models are available, what changes in habitat are projected?
  - Is the area projected to remain a suitable vegetation type (i.e. forest for forest species)?
  - Is the projected vegetation type(s) within the area identified as climatically suitable by climatic niche models also suitable for the target?
  - Does the target's current range overlap with projected future vegetation types?
  - If conversions (e.g. grassland to forest) are projected, which factors drive these conversions?
  - How sensitive are the results to different climate scenarios?
  - If multiple projections based on different vegetation models are available, is there a consensus among projections?

- Evaluate projected changes to relevant disturbance regimes (e.g. fire, flooding etc.)
  - Is the species sensitive to a particular disturbance regime?
  - How is climate change projected to impact that regime?
- What ecological relationships, if any, constrain the abundance and distribution of the target? Use conceptual models, natural history, and spatial models to answer the following:
  - Evaluate potential impacts to interspecific relationships (e.g. mutualist species such as pollinators, seed dispersers, prey or forage species, predators, parasites and diseases, etc.)

- How will climate affect these interacting species (using known relationships or climatic niche models when available)?
    - Stable
    - Improve
    - Degrade
- Could changing climate conditions introduce new species such as new predators, diseases, or competitors?
- Are spatial changes to the interacting species likely to be similar or different to the target (e.g. both expand upslope)?
- Do the interacting species respond to similar climate variables?
- Do projected climate conditions change existing relationships (e.g. switch competitive advantages, increased virulence of disease)?

Evaluating Non-climate Stressors

While climate change is expected to be one of the most significant drivers of species imperilment over the next century (Thomas et al., 2004), non-climate factors such as habitat loss and fragmentation, nitrogen deposition and acid rain, and invasive species are also key drivers of biodiversity loss (Purvis et al., 2000; Sala et al., 2000). Non-climate drivers affect the viability of species and ecological systems in the absence of climate change, and in some cases may present a more immediate threat to the conservation target's viability (Sala et al., 2000). However, in all cases, climate change will likely have an additive or even synergistic interaction with existing threats (Brook et al., 2008; Opdam and Wascher, 2004; Potts et al., 2010) and reducing non-climate stresses is the third most often cited climate adaptation action (Heller and Zavaleta, 2009). At a most basic level, species with populations already reduced by habitat loss and invasive species may face additional habitat loss from climate-induced range contraction (Wenger et al., 2011). Climate change can also amplify the impacts of habitat fragmentation by limiting the ability of species to track changing climate conditions (Wilson et al., 2007). These and other interacting effects demonstrate the need to identify and account for non-climate factors as both independent and interactive contributors to climate vulnerability. Non-climate factors generally affect the adaptive capacity of a species or system, but could conceivably also alter sensitivity or exposure.

One of the biggest challenges to incorporating non-climate factors is that these stressors will also change over time in ways that are difficult to predict. Where possible, including projections for population growth and land-cover change in the focal region can help provide a sense of projected landscape changes over time (e.g. Baker et al., 2004; Waddell, 2002). The following questions can be used to help evaluate non-climate stressors:

- What non-climate stressors (e.g. land conversion, grazing, logging, environmental toxins, etc.) currently or potentially impact the conservation target?
- Compared to climate change, are these stressors more or less important? Are these stressors a more immediate threat than climate change?
- Will climate change alter the dynamics of these stressors? For example, will reduced precipitation influence agricultural productivity and alter the profitability of farm land?

RESOURCE RESPONSE SCENARIOS

Ecosystems are characterized by complex, non-linear, interactions between biotic and abiotic factors and historical contingencies that operate at multiple scales (Gunderson, 2002). This complexity challenges our ability to predict future ecological conditions based on observations of past behavior (Peterson et al., 2003). The uncertainty associated with climate change exacerbates the complexity of ecosystem management. For example, climate change has already led to the emergence of a previously insignificant but now devastating disease, the Chytrid fungus (Pounds et al., 2006) and increased the frequency and severity of mountain pine beetle outbreaks in whitebark pine (Bentz et al., 2010). Evidence from the fossil record shows that ecosystems did not shift as one unit, but rather that individual species responded uniquely to past climate change (Jackson and Overpeck, 2000). This reshuffling will result in new biological communities and unexpected interactions among species, challenging our ability to project ecosystem change effectively (Gilman et al., 2010). For example, although species range shifts are likely to alter the range or impact of invasive species, it is difficult to predict specific cases (Hellmann et al., 2008).

Adaptation plans that rely too heavily on a single model, assessment type, or projected future are likely to miss important potential impacts and leave managers unprepared for surprises (Holling and Meffe, 1996; Peterson et al., 2003). Similarly, while is it useful to identify the “most likely” scenario by focusing on where models agree, an adaptation plan will be more robust if it includes model or assessment results that disagree with the majority. This is because it is very difficult to judge which models best capture future dynamics (Littell et al., 2011).

Developing several alternative scenarios that present the range of plausible futures is one approach that can help managers develop robust plans (Peterson et al., 2003).

Formal scenario development begins with the identification of a small number (1-3) of the most important and uncertain driving forces that influence the conservation target's viability (Peterson et al., 2003). The vulnerability assessment can help identify these forces. For example, projected changes in spring precipitation may be both critical to the conservation target and highly uncertain according to climate model projections. A species' ability to track climate change may be dependent on landscape connectivity, which depends on land-cover change. Climate change may significantly increase the prevalence of a devastating disease. Managers can use this information to develop a range of hypothetical but plausible futures based on differing assumptions as to how these driving forces will behave and how the conservation target may respond.

One simple approach is to develop scenarios based on how the target may respond to climate change. Dawson et al. (2011) identified four fundamental ways that species have responded to climate change historically: 1) tolerate change and remain *in situ*, 2) undergo habitat shifts by moving short distances (1to 10 km), 3) migrate long distances (100-1000 km) or 4) become extinct (or extirpated from the focal area). For managers focused on a defined geographic region, these four outcomes broadly translate into managing the target *in situ*, facilitating short or long distance movements, or managing transformation to a new system. The vulnerability assessment can provide insight into which of these outcomes (or combinations of outcomes) is most likely, and therefore where to focus management and planning efforts. However, given the limitations of model projections and our current ability to accurately project how ecosystems will respond to climate change, plans that address a range of plausible outcomes will be more robust to future uncertainty.

Once alternative futures are constructed, planners can identify management actions that would benefit the management target within each scenario. Actions that are beneficial regardless of the scenario are considered robust and are therefore a high priority (Snover et al., 2007). Some actions may be important, but only be necessary or effective for one scenario or only under a specific set of circumstances. In this case, developing a plan that allows for flexible implementation of these actions can increase preparedness without committing too many resources to a potentially ineffective, or worse harmful, management strategy (Millar et al., 2007). For example, managers may want to develop a rough plan for assisted migration that identifies potentially relocation sites and outlines risks and implementation issues, but wait to develop a full plan and certainly wait to implement the plan until it becomes clear that such an action is necessary. Actions that can be implemented but reversed or stopped if necessary are also flexible (Snover et al., 2007). For example, annual prescribed burning can be implemented until it appears unnecessary or ineffective at which point burning can be halted. In addition to flexibility and robustness, other commonly used criteria can also be used to prioritize actions such as effectiveness, cost-benefit ratio, social and political feasibility, and departure from current management practice (Cross et al., 2012; Snover et al., 2007).

CASE STUDY

An Assessment of Climate Vulnerability and Adaptation Strategies for Oregon white oak (*Quercus garryana*) in the Willamette Valley Ecoregion of Oregon

The following case study provides an illustration of how the vulnerability assessment checklist and resource response scenarios can be used to inform adaptation planning. The management objective for the case study is defined as maintaining the extent of Oregon white oak (*Quercus garryana*) woodlands in the Willamette Valley. *Q. garryana* is a foundation species in the oak woodlands of the Willamette and a priority conservation target for this region. This management objective was identified in a climate adaptation workshop funded by the North Pacific Landscape Conservation Cooperative and conducted with the Fish and Wildlife Service and Willamette Valley stakeholders in August 2012. As part of this workshop, participants developed a conceptual model of critical drivers of oak woodland extent, which was used to structure this case study (Figure 3.2).

DIRECT CLIMATE IMPACTS

To evaluate direct climate impacts to *Q. garryana*, I first summarize projected climatic changes for the Willamette Valley using downscaled (~ 1-kilometer) results from five General Circulation Models, or GCMs: the Community Climate Systems Model version 3 (CCSM3) (Collins et al., 2006), the Canadian Center for Climate Modeling and Analysis model CGCM3.1 (t47) (Zhang and McFarlane, 1995), GISS-ER (Schmidt et al., 2006), Hadley CM3 (Gordon et al., 2000), and MIROC3.2 (medres) (K-1 Model Developers, 2004) (Shafer and Bartlein, 2011). These models were run using two emissions scenarios developed in the Third IPCC Assessment, namely the A2 (a relatively high emissions scenario resulting from a heterogeneous world with high population growth, slow economic development and slow technological change) and A1B (a medium emission scenario resulting from rapid economic growth and rapid technological change in the direction of both fossil-intensive and non-fossil energy resources) (Nakicenovic and Swart, 2000). Projected future climate conditions reported here are averaged for the time period 2070-2099, referred to as the "2080s" from here on. Reported historical conditions are averaged for the years 1961-1990 using data derived from the CRU CL 2.0 (New et al., 2002) and CRU TS 2.1 (Mitchell and Jones, 2005) climatology datasets (Shafer and Bartlein, 2011). All reported projected changes to specific climate variables (e.g. temperature and precipitation) were calculated using this dataset as a baseline throughout the case study.

I review changes in climate variables that directly affect *Q. garryana* viability and compare any known thresholds to projected conditions. Lastly, I review projected range shifts for *Q. garryana* modeled using climatic niche models based on the Random Forest classification tree procedure (Case and Lawler, 2012). Projected range shifts are for the year 2100 and are based on downscaled (~1-kilometer) climate projections from five climate models (BCCR BCM 2.0, CCCMA, CGCM 3.1, CSIRO MK 3.0, INMCM 3.0, MIROC 3.2 (Medres)) and the A2 emissions scenario (Nakicenovic and Swart, 2000). Note that the five models used by Case and Lawler mostly differ from those used to assess projected climate changes.

Projected Climate Changes for the Willamette Valley

There is good qualitative agreement among the ten climate projections (five models and 2 emissions scenarios) reviewed in this study for the Willamette Valley. In addition, these projections qualitatively agree with published assessments of future PNW climate changes (Mote and Salathe Jr, 2010; Rogers et al., 2011). By the 2080s, the models agree that all seasons are projected to be warmer, with summer temperatures increasing slightly more than winter. The mean annual temperature in the Willamette is projected to increase 6.2 °F and projections from five individual climate models and two emissions scenarios (A1B and A2) project a temperature increase ranging from 2.7 to 7.9 °F by the end of the century (Table 3.1). This projected change is slightly lower than the global projections for the same emissions scenarios of 3.1 to 9.7 °F (IPCC, 2007a).

Most (six out of ten) climate projections show increased precipitation annually, but four projections (CCSM3 and Hadley CM3 for both emissions scenarios each) show a decrease. Net annual precipitation based on the ensemble mean of all models is projected to increase 3% for the A2 scenario and 2% for the A1B scenario. Individual projections of change to mean annual precipitation range from -9% to 16% by the end of the century. Seasonally, the majority of models project warmer, wetter winters and hotter drier summers. All model and scenario combinations project drier summers and there is good agreement (six, or more depending on the season, out of ten projections) that the other three seasons will be wetter (Table 3.1).

To put these climate changes in perspective, the projected end-of-century mean annual temperature and precipitation for the Willamette Valley are roughly analogous to those currently found in northern California around the northern edge of the central valley. Seasonal precipitation in this region of northern California also appears to be roughly within the range of future projections for the Willamette, although current California summers are still drier than projected summer conditions for the Willamette.

Natural History and Direct Climate Sensitivity

Q. garryana's current range spans from south-central California to southern British Columbia and occupies sections of the Puget Sound Trough and Willamette ecoregions as well as extending east through the Columbia Gorge and northward from the Gorge on the east side of the Cascade range (Larsen and Morgan, 1998). *Q. garryana* can tolerate a range of soil moisture conditions, but is generally more competitive on dry sites (Stein, 1990). Consequently, this species is ranked as having a fairly low physiological sensitivity to climate. Adaptive capacity through reproduction is also low due to the slow reproductive cycle of this species (Case, 2013).

Projected mean annual temperature and precipitation values for the Willamette Valley are within the current range tolerated by *Q. garryana* (8° to 18° C (46° to 64° F); and 170 to 2630 mm). This species does not require or benefit from cold temperatures during winter so warmer winter temperatures are unlikely have a significant impact. *Q. garryana* has been observed to tolerate temperatures of up to 116°F (Stein, 1990). The maximum projection for the mean warmest month is 80°F, which is still below the current range for July temperatures of 60° to 84°F (Stein, 1990).

It is important to note that while projected temperatures fall within the current range occupied by *Q. garryana*, this does not mean that the population in the Willamette Valley is adapted to these warmer climatic conditions. Plant population area generally adapted to local climate conditions, and this regional specialization has implications for range shifts in response to climate changes (Davis and Shaw, 2001). In addition, the climate statistics reported here do not provide information about the frequency or intensity of extreme heat wave events. In general, extreme heat events are likely to increase (Meehl and Tebaldi, 2004). Extreme heat waves have adversely affected oak systems in Europe (Ciais et al., 2005) and could have similar negative effects in the Willamette (Bachelet et al., 2011).

Q. garryana is drought tolerant and so generally benefits from warmer and drier conditions (Bachelet et al., 2011; Hansen, 1947; Sprague and Hansen, 1946; Stein, 1990). In fact, *Q. garryana* woodlands were more widespread throughout western Oregon and Washington during the Holocene (circa 11,000 – 7,250 YBP) when conditions were warmer and drier than they are today (Peterson et al., 1997; Walsh, 2008). Competitive pressure from Douglas-Fir (*Pseudotsuga menziesii*) may increase when growing season precipitation (Apr-Sep) exceeds 250 mm (Larsen and Morgan, 1998). Contemporary precipitation in the Willamette Valley for the approximate growing season (Mar-Aug) is 379 mm. Eight out of the ten climate projections indicate that precipitation for this time period will decrease slightly, but none of the projections indicate that growing season precipitation will drop below 250 mm in the Willamette Valley. While this drying trend may not be significant enough to confer a competitive advantage over *P. menziesii*, it is unlikely to disadvantage *Q. garryana* either (Bachelet et al., 2011).

Changes in winter precipitation could also affect oak ecology. Some climate models project both an increase in winter precipitation and a northward shift in storm tracks which could lead to an intensification of winter precipitation events (Salathé, 2006). Intense storms could cause landslides and wind throw leading to the loss of adult oak trees (Bachelet et al., 2011). Wind may be a particular threat to large oak trees in open prairie fields.

While at a broad scale the climate is likely to remain suitable for *Q. garryana* as a species, climate changes are likely to have a potentially significant impact on oak community composition. Riegel et al. (1992) found that *Q. garryana* community structure is strongly driven by precipitation. Specifically, in southwest Oregon, oak communities in regions with less than

1000 mm of mean annual precipitation are more similar to those found in California, while those with greater than 1000 mm are more similar to the types currently found in the Willamette Valley. Over the last 30 years, mean annual precipitation in the Willamette has remained above 1000 mm and the majority of climate models used in this study project that mean annual precipitation will increase. By this measure, it appears that precipitation may be too high to support California-type oak communities, although one climate scenario (A2, CCSM3) does project a decrease in mean annual precipitation, which would drop the Willamette Valley below the 1000 mm threshold.

Climatic Niche Model Projections

Climatic niche model projections for the 2080s, based on five climate scenarios using the A2 emissions levels, agree that the vast majority of *Q. garryana's* current range will remain climatically suitable and will, in fact, expand to the east and west. In addition, all five projections agree that climatic conditions will remain stable for *Q. garryana* within the Willamette Valley (Figure 3.4). Higher elevation areas to the east and west may become climatically suitable providing an opportunity for oaks to expand upslope and east of the Cascade Mountains.

The following climate variables were most important when modeling the historical distribution of *Q. garryana* (listed in order of decreasing importance):

1) Temperature difference: the difference between the mean warmest month temperature and the mean coldest month temperature
2) Fall precipitation
3) December precipitation
4) Winter mean maximum temperature

5) July mean maximum temperature
6) Summer mean maximum temperature

For climatic niche models, these variables were significant drivers of current *Q. garryana* distribution and so, monitoring changes in these variables could provide insight into the direction and rate of climate change for this species.

Summary of Direct Climate Impacts

Current evidence suggests that, at a broad scale, the Willamette Valley climate will remain suitable or even improve for *Q. garryana*, at least into the 2080s. There is unanimous agreement among climate projections that temperatures will increase but are very likely to remain within the general range tolerated by this species. There is less certainty associated with precipitation, but there is good model agreement that fall, winter and spring will be wetter and summers will be drier. These changes are unlikely to disadvantage *Q. garryana* and may benefit this species (Bachelet et al., 2011). However, climate events that occur at fine spatial and temporal scales such as the frequency of extreme heat waves, wind and rain storms may affect climate suitability for this species but are not captured in the Global Circulation Models. Some authors suggest that these events will increase in frequency (Ciais et al., 2005; Meehl and Tebaldi, 2004; Westerling et al., 2006). If so, these fine scale events could increase *Q. garryana* mortality and alter oak community composition.

INDIRECT CLIMATE IMPACTS

While direct climate conditions appear likely to remain stable, historically, climate has not been the most significant factor determining the abundance and distribution of *Q. garryana*

(Hansen, 1947). The interacting effects of summer drought, fire regime, and CO_2 fertilization conditions are all likely to affect oak ecology and its ability to compete with conifers. To assess indirect climate impacts, I first review projected changes to the general vegetation within the Willamette Valley. Available datasets for evaluating vegetation change include the results of a climatic niche model projecting shifts in biome vegetation types (Rehfeldt et al., 2012), and projected changes to general vegetation types using the MAPSS-CENTURY 1 (MC1) DGVM. The DGVM can provide insight into projected changes to fire regime and the implications of decreasing precipitation and increasing CO_2 concentrations for general vegetation type. I then use a literature review to assess potentially significant ecological interactions that influence *Q. garryana's* sensitivity and adaptive capacity including: herbivory, seed dispersal, and insect, disease and fungal pests.

Projected Changes to Willamette Valley Vegetation

Q. garryana currently occupies a range of habitat types including open grasslands, prairies, grassland balds and the ecotone between conifer forest and grassland (Larsen and Morgan, 1998; Sprague and Hansen, 1946; Stein, 1990). In the Climate Change Sensitivity Database, these habitat types are referenced as extremely sensitive to climate change (Case, 2013). In this region, *Q. garryana* can be found intermixed with conifer forest, particularly *P. menziesii*, but is considered shade intolerant and eventually will die off under conifer cover (Devine and Harrington, 2006). Historically, people have used small frequent fires to maintain oak woodlands in the Willamette (Boyd, 1999). In the PNW, maintaining a mix of grassland and conifer sites is important for providing ecotonal habitat and also provides favorable habitat for squirrels and jays that disperse oak acorns (see Chapter 2). Given its wide latitudinal range, *Q. garryana* is associated with a wide range of vegetation community types (Stein, 1990).

Climatic Niche Model Projections of Vegetation Biome Shifts

Rehfeldt et al. (2012) mapped projected range shifts for 46 North American biomes using three Global Climate Models each using two emissions scenarios (for a total of six future climate scenarios): Canadian Center for Climate Modeling and Analysis, using CGCM3 (T63) with emissions scenarios A2, and B1; Met Office, Hadley Centre, using Hadley CM3 and emissions scenarios A2 and B2; and Geophysical Fluid Dynamics Laboratory, using CM2.1 and emissions scenarios A2 and B2. Climatic niche models were developed using a Random Forest tree classification algorithm which uses a model averaging approach. The model defines the contemporary climatic niche for each biome type and identifies the location of that niche under projected future conditions. The model also identifies areas that have a future climate with "no-analog" in the present North American climate. The authors compiled a "consensus" map showing the vegetation type on which the majority of the six climate projections agreed, ignoring no-analog results (ties were decided randomly).

The modeled historical distribution for *Q. garryana* developed by Case and Lawler (2012) overlaps with five contemporary vegetation biomes, as modeled by Rehfeldt et al.: Oregon coastal conifer forest, Oregon deciduous and conifer forest, Cascade-sierran montane conifer forest, California chaparral, and California evergreen forest and woodland (Figure 3.5). The consensus projected vegetation for the 2090s shows the majority of the Willamette Valley ecoregion converting from Oregon coastal conifer forest and Oregon deciduous and evergreen forest to Cascade-sierran montane conifer forest (Figure 3.6). A small area in the northwest of the Valley remains Oregon deciduous and evergreen forest with small amounts of California chaparral. Individual vegetation projections for the A2 emissions scenario also show significant conversion to Cascade-sierran montane conifer forest with some amount of California chaparral and California evergreen forest and woodland. Except for the A2 CGCM3 model projection, very little of the Willamette is projected to experience no-analog climates. These projections all suggest change in the general vegetation biome type within the Willamette will change, under some scenarios dramatically (e.g. to California chaparral). The current range for *Q. garryana* overlaps with all projected future biome types, except, of course the no-analog. This suggests that there may currently be oak communities with associated vegetation types similar to those that may move into the Willamette Valley in the future. Identifying examples of California chaparral, California evergreen forest and woodland, and Cascade-sierran montane conifer forest that currently sustain *Q. garryana* populations, if such associations exist, could provide insight into future vegetation community structure and interactions. Figure 3.3 shows where *Q. garryana*'s current range overlaps with areas in southern Oregon and northern California that have mean annual temperatures and precipitation conditions similar to those projected for the Willamette Valley in the 2080s. These areas could potentially serve as reference sites for learning about associated vegetation communities that may be suitable under new climate conditions.

<u>Mechanistic Projections of Changes to Vegetation Types</u>

Rogers et al. (2011) projected vegetation changes using the MAPSS-CENTURY 1 (MC1), a dynamic global vegetation model particularly designed to model fire dynamics. All model projections shared here are for the 2080s (yearly average from 2070 – 2099). To test model validity, Rogers et al. (2011) modeled historical vegetation types and compared the results to maps of existing potential vegetation (based on Küchler, 1964). While the modeled vegetation matched existing vegetation well overall, it failed to recreate the mixed open forests of the Willamette valley. The authors attribute this failure to the human-modified fire regime in this region which historically maintained open oak forests. Given that the model did not accurately predict known vegetation types, projections of future vegetation using this model may also be less accurate for the Willamette Valley. Another interpretation is that the Rogers et al. (2011) vegetation projections for the Willamette illustrate future vegetation conditions in the absence of human fire management.

Rogers et al. (2011) used data from three different climate models, all of which used the A2 emissions scenario (a mid-high emissions scenario): CSIRO Mk3 (Gordon et al., 2000), MIROC 3.2 medres (K-1 Model Developers, 2004), and Hadley CM3 (Johns et al., 2003) (hereafter referred to as CSIRO, MIROC and Hadley respectively). The CSIRO, MIROC and Hadley climate projections differ primarily in their summer conditions. CSIRO projects mild temperature increases and more precipitation overall, with minimal decrease in summer precipitation. In contrast, both MIROC and the Hadley model project hotter temperatures year round and drier summers. The Hadley model is more extreme projecting much hotter and drier summers than the MIROC. Subsequently, summer water stress decreases according to the CSIRO model, but increases for both the MIROC and Hadley models. Similarly, Net Primary Productivity (NPP) increases during fall, winter and spring in all three models and slightly during summer for the CSIRO model, but decreases during the summer in the MIROC and Hadley models (Rogers et al., 2011).

According to the modeled historical vegetation, the portion of *Q. garryana's* contemporary range (as modeled by Case and Lawler, 2012) included within Rogers et al.'s study area is almost entirely classified as maritime evergreen needle-leaf forest (Figure 3.7). The exception to this is the *Q. garryana* population on the east side of the cascades, near the Columbia Gorge, which overlaps with temperate evergreen needle-leaf forest. The three different climate scenarios produce very different vegetation projections, despite using the same vegetation model (MC1). Due to the mild changes projected by the CSIRO model, this model projects no change for the vegetation in the Willamette valley, which remains maritime evergreen needle-leaf forest. The very hot and dry Hadley model projects a conversion to temperate evergreen needle-leaf forest more similar to conditions currently found on the east side of the mountains. Given the current overlap of *Q. garryana's* range with the temperate forest type, this general vegetation type is likely to still be suitable for oak. Lastly, the MIROC model projects that the Willamette vegetation will largely transform into subtropical mixed forest and temperate warm mixed forest (Figure 3.7) (Bachelet et al., 2001; Rogers et al., 2011). There is a very small overlap between *Q. garryana's* present range and the subtropic and temperate warm forest types (seen in the extreme southwest corner of the modeled historical vegetation in Figure 3.7). However, the overlap is so small that it is not clear whether it is meaningful. Rogers et al.'s study area did not extend into California. However, in northern California, *Q. garryana*'s current range overlaps with significant areas of California mixed forest types (Küchler, 1964).

While the general vegetation types projected by the MC1 model are all within the historical range of *Q. garryana*, conifer competition and fire regime have historically had a very significant impact on oak habitat suitability. The MC1 model can provide some insight into how these ecological processes may be affected by climate change. Specifically, the MC1 model projects that summer droughts and the frequency and intensity of wildfires will both increase. These changes have complex implications for oak ecology. Increased summer drought may give the drought tolerant *Q. garryana* a competitive advantage over *P. menziesii* (Sprague and Hansen, 1946; Taylor and Boss, 1975). In addition, frequent low intensity burns historically maintained oak woodlands in this region (Boyd, 1999) and prescribed burns are a potentially important, though controversial, component of current oak restoration and maintenance efforts (Hamman et al., 2011). The MC1 projects an increase in the total area burned and burn severity in western Oregon under all climate scenarios (Rogers et al., 2011). However, while low intensity burns have been beneficial, high intensity burns can have a detrimental impact on overall oak and prairie community structure in altered and degraded oak habitats (Agee, 1996). In addition, Bachelet et al. (2001) found that while increased wildfire and summer drought could theoretically lead to more grasslands in western Oregon, increased CO_2 fertilization increases water use efficiency of trees. The balance between these drivers appears to favor tree growth. Consequently, CO_2 fertilization may benefit conifer species and decrease the competitive advantage of *Q. garryana* despite drier growing season conditions (Bachelet et al., 2011).

Potential Climate Impacts to Biotic Interactions

The Climate Change Sensitivity Database identifies *Q. garryana* as being highly sensitive to climate change due to limited dispersal ability and disturbance regimes including disease, pests, and pathogens (Case, 2013). In addition, herbivory can have a significant impact on vegetation structure in general (Côté et al., 2004) and in oak systems in particular (Larsen and Morgan, 1998; MacDougall, 2008; Rousset and Lepart, 1999). Here I review potential impacts climate may have on the following biotic interactions: seed dispersal and predation, herbivory, and pest species.

Seed Dispersal and Predation

Eastern gray squirrels (*Sciurus carolinensis*), western gray squirrels (*Sciurus griseus*), Douglas Squirrels (*Tamiasciurus douglasii*) and Steller's jays (*Cyanocitta stelleri*) disperse and bury oak acorns. These actions benefit oaks by spreading seeds to new locations and improving germination success respectively (Fuchs et al., 1999; Larsen and Morgan, 1998). Climate change is unlikely to negatively affect these squirrels and jays given their broad geographic ranges and generalist behavior. In addition, each of these species responds to slightly different environmental conditions and operates at slightly different spatial scales. As a result, impacts to one species may be compensated for through the dispersal actions of another (Elmqvist et al., 2003).

It is possible that a warmer climate could benefit squirrel and jay dispersers, for example by reducing winter mortality, but no studies have explicitly investigated this possibility. Higher densities of squirrels and jays could lead to both higher dispersal rates (more acorns dispersed longer distances), which would benefit oaks, but also higher predation rates as competition for acorn resources increases, which could reduce reproduction (Chapter 2). Approximately every third year, *Q. garryana* produce a mast crop of acorns (Peter and Harrington, 2009) presumably to overwhelm predation pressure. Mast acorn production is a successful strategy for satiating seed predators and increasing germination and seedling production in other oak systems (Pérez-Ramos and Marañón, 2008). Consequently, the net impact of changes to squirrel and jay abundance are both highly uncertain and likely to be small.

Oaks are considered dispersal limited (Stein, 1990). Heavy acorns will essentially only disperse beyond the parent canopy if moved by squirrels or birds or through gravity if located on a steep slope. Observations of Steller's Jays have found that these birds will move *Q. garryana* acorns up to 600 meters from adult trees, possibly up to 1 kilometer (Fuchs et al., 1999). Studies of jay dispersal of other heavy seeds have estimated maximum dispersal distance of about 1 km for holm-oak (*Quercus ilex*) dispersed by the European jay *Garrulus glandarius*, (Gómez et al., 2008); 4 km for smaller Beechnuts (*Fagus grandifolia*) dispersed by Blue jays (*Cyanocitta cristata*) (Johnson and Adkisson, 1986), and ~1 km for *Quercus palustris* acorns dispersed by Blue jays (Darley-Hill and Johnson, 1981). Jays will move longer distances if scattered trees or fencerows are present as stopping points (Fuchs et al., 1999; Gómez et al., 2008). In addition, squirrels and jays in the PNW both prefer to cache acorns under conifer forest cover (Fuchs et al., 1999, Chapter 2). Consequently, the presence of conifer grassland edges and scattered conifer trees may facilitate dispersal of oak acorns to new locations. Even with these measures however, expansion of *Q. garryana* into new habitat is likely to be extremely slow due to the low probability of long distance (e.g. 1 km) dispersal events. If rapid colonization of new habitat areas is desired, planting seedlings or dispersing acorns by hand are likely to be necessary management actions.

Herbivory

Q. garryana leaves are particularly nutritious browse for deer and elk (Larsen and Morgan, 1998) and high densities of these species may limit recruitment (MacDougall, 2008). Habitat suitability models project that the Willamette valley will remain climatically stable for Mule Deer (Langdon, 2013). Warmer winters have been shown to benefit deer populations through increased body mass and decreased winter mortality (Côté et al., 2004). Increased deer population could have a negative effect on oak recruitment. The degree of this effect would depend on the extent to which deer populations increase. Unchecked ungulate herbivory can have significant detrimental impacts on forest regeneration and structure (Côté et al., 2004; MacDougall, 2008). While impacts of increased herbivory could be large, projected effects of climate on deer populations are uncertain. In addition, deer management actions that could reduce overpopulation are well developed and understood.

Insect, Disease, and Fungal Pests

Oaks host numerous insects, pathogens, and fungi, which damage leaves and acorns. In the case of *Q. garryana*, currently, these rarely cause tree mortality (Stein, 1990). However, insect species are physiologically highly sensitive to climate, which has a strong influence on insect metabolic rates, fecundity, and dispersal. Warmer winter temperatures and a longer growing season may increase insect population sizes (Dukes et al., 2009). In particular, warmer temperatures may lead to longer and larger tent caterpillar outbreaks (Roland et al., 1998). Changes in the geographic distribution of insect herbivores could put oaks in contact with new pests (Garrett et al., 2006). In addition, warmer temperatures may alter the timing of insect hatching in relation to leaf bud burst or acorn maturation. This could benefit or harm insect populations with cascading effects on oak acorns and reproduction. Some have argued that the net impact of warming temperatures will be to increase disease and pest pressure (Harvell et al., 2002).

Discula quercina is an endophyte, or a symbiotic fungi, of *Q. garryana*. Infecting spores are spread by rain. Infection rates increase during the spring rainy season, and new infections halt once spring rains end and summer dry period begins. Duration of the rainy period is probably the most important driver and a longer rainy period may lead to increased infections. While *D. quercina* appears harmless, even potentially beneficial, to *Q. garryana*, it can infect and damage *P. menziesii* (Wilson and Carroll, 1994). As this fungus is spread by rain, changes in the duration of the rainy season driven by climate change could affect its prevalence, but no studies have investigated this potential impact directly.

The impacts of climate change on plant insect herbivores and pathogens are extremely complex, highly uncertain, and poorly studied (Dukes et al., 2009; Garrett et al., 2006). Ultimately, the potential impact of new or more virulent diseases or parasites on *Q. garryana* could be large, but is highly uncertain and no current studies identify a specific threat.

Summary of Indirect Climate Impacts

Overall, while climatic changes, such as increased summer drought and fire frequency, may improve conditions slightly for *Q. garryana*, it is not clear whether these changes will favor grassland habitat or be sufficient to confer a competitive advantage over *P. menziesii*. Specifically, CO_2 fertilization may improve the drought tolerance of *P. menziesii*, reducing any advantages *Q. garryana* would gain from drier conditions. Consequently, while the Valley is likely to remain climatically suitable for *Q. garryana*, active management of competition with *P. menziesii*, or other conifers, is likely to still be necessary.

Regardless of whether the region remains suitable for *Q. garryana* as a species, the vegetation community of the Willamette Valley is projected to change significantly. The modeled vegetation changes reviewed here show a wide range of potential future vegetation conditions in the Willamette Valley. The contemporary climatic range of *Q. garryana* overlaps with all projected vegetation types, suggesting that none of these potential future vegetation types categorically precludes suitability for this species. However, *Q. garryana's* actual distribution is severely restricted within its overall climatically suitable range (Larsen and Morgan, 1998), and so overlap of current geographic range does not ensure that these alternative vegetation types provide suitable habitat conditions for *Q. garryana*. In addition, *Q. garryana* is associated with fine-scaled habitat features such as grassland balds and the ecotone between grasslands and conifer forest. The two vegetation models reviewed here operate at a broad spatial scale that does not capture these types of features. Finding examples of contemporary oak communities within each of the potential future vegetation types, if possible, could provide insight into future oak woodland community types and competitive or other ecological interactions that may affect oak persistence in the Valley.

The consensus from the climatic niche model projections shows the majority of the Willamette Valley converting from Oregon coastal conifer forest and Oregon deciduous and evergreen forest to Cascade-sierran montane conifer forest (Figure 3.6). Refeldt et al.'s historical projections show Cascade-sierran montane conifer forest as present at higher elevations (relative to the Willamette) on both sides of the Cascades. Given that projected temperatures and summer drought are expected to increase, it seems likely that projected changes refer to examples of this vegetation type on the east side of the Cascades (Figure 3.5). This projected change is very similar to the MC1 projections under the Hadley model, which also show an expansion of temperate evergreen needle-leaf forest currently present on the east side of the Cascades (Figure 3.7). Under some climate scenarios, both the MC1 and climatic niche model also project an intrusion of California mixed forest type (temperate warm mixed forest and subtropical forest using the MC1 model and California evergreen forest and woodland using the niche model).

Lastly, the Willamette experiences no qualitative change under the relatively mild changes projected under the CSIRO climate scenario using the MC1 model (Figure 3.7).

In addition to possible changes to general vegetation type, climate may affect viability of *Q. garryana* indirectly by influencing important life history events such as acorn dispersal, seedling recruitment and herbivory. Changes in the distribution or abundance of animals mediating these processes could have potentially significant impacts on oak survival in this region. Currently, formal studies have not investigated how climate change may impact these species and their relationship with *Q. garryana*, in general or within the Valley. Given their generalist behaviors, climate change is less likely to adversely impact these species. There is some limited evidence that warming may benefit deer, but whether such a benefit will materialize, and whether changes will be significant enough to have a measurable impact on oak regeneration, is highly speculative at this point.

NON-CLIMATE STRESSORS

The population in the Willamette valley is expected to almost double by 2050 to roughly 4 million. Baker and others (2004), in conjunction with stakeholders, developed three scenarios for how development might occur to accommodate these almost 2 million new residents. These scenarios are not predictions of future development but rather different visions of how future development might occur. The three scenarios were "plan trend" in which current development trends continued, "development" in which current planning policies were loosened, and "conservation" in which ecosystem protection and conservation were given high priority. Stakeholders agreed that, overall, environmental and resource protections would remain largely in place. In all three scenarios, the stakeholders felt that most development would take place primarily on existing agricultural lands rather than converting native habitats. Consequently, the direct loss of native habitat is small in all scenarios. However, in the conservation scenario, rural development is clustered which reduces the amount of agricultural land conversion and the extent of contact between rural residential lands and native habitats. Also in the conservation scenario, some agricultural lands are restored to native habitats.

These scenarios, while not predictions of the future, provide a range of plausible future development trends. The overall picture is one in which native habitats are generally protected, at least from direct conversion. While this may be optimistic, it is the collective vision developed by a diverse group of stakeholders and therefore represents at a minimum the preferred general future for the Valley (Baker et al., 2004). If this is the case, the threat of direct conversion may be lower than the threat of development encroaching upon protected native habitats. Urban encroachment can have numerous impacts on protected areas including loss of connectivity, spillover of invasive or nuisance species, increased recreational use, and altered micro-climatic conditions at the protected area edge (Hansen et al., 2005). For *Q. garryana* specifically, urbanization appears to negatively affect dispersal processes as acorn predation is higher and dispersal distances are shorter in urban oak woodlands (Chapter 2). Indirectly, regional land use patterns may impact fire management. While wildfire may be more likely, fire suppression is more likely and prescribed burns more difficult to implement in densely populated areas. Lastly, much of *Q. garryana* is on private lands in the Willamette and private landowners may favor the commercially valuable *P. menziesii* over *Q. garryana*, and so actively remove oaks or facilitate *P. menziesii* establishment on their lands (Fischer and Bliss, 2006).

RESPONSE SCENARIOS AND ADAPTATION STRATEGIES

Multiple lines of evidence suggest that the Willamette Valley will continue to support *Q. garryana*, at least to the end of the century, despite climate change. This conclusion is based on projected continued climatic suitability and a lack of compelling evidence for drastic habitat and ecological changes that would categorically exclude this species from the Valley. However, numerous uncertainties remain. The models reviewed above are not able to capture fine-scaled changes to local habitat conditions such as grasslands and balds which are critical oak habitat. The increased prevalence of fire and summer drought could benefit *Q. garryana* by decreasing competition with *P. menziesii* and other conifers. Improved climate conditions could allow oaks to colonize new locations and expand their current range (Figure 3.4). Conversely, severe fires and wind storms may increase oak mortality. Colonization and regeneration may be limited by a lack of long-distance dispersal events. Drought sensitive tree species may gain an advantage over oaks through CO_2 fertilization.

To identify strategies for oak management that encompass the uncertainties listed here, I developed a series of three resource response scenarios: 1) stability, 2) expansion, and 3) contraction based on a wide range of plausible outcomes identified as part of the vulnerability analysis. Strategies are given high priority if they either address a likely change or if they are beneficial regardless of how climate changes in the future (i.e. they are robust to future scenarios). Other actions are given a low priority. The following recommendations are aimed at developing a climate adaptation plan for *Q. garryana* as a species. Conservation of western oak-prairie systems in the face of climate change has been well reviewed elsewhere (Bachelet et al., 2011).

Resource Response Scenario: Stability

This scenario is based on the balance of evidence, which suggests that it will be feasible to maintain *Q. garryana* in the Willamette Valley using the same basic management strategies that are in place today. Competition with conifers is likely to continue to be a challenge for management, as it is today, but unlikely to increase to the point that management is no longer feasible. Warmer, drier summers benefit oak and decrease competitive pressure slightly, but overall the need for management intervention remains. While conditions remain stable for *Q. garryana* as a species, the existing population is not well adapted to the warmer temperatures.

The comparatively mild projected climate changes also suggest that variation in microclimate may be sufficient to provide climate refuges for this species under a range of changing conditions. While most current management strategies are likely to be applicable, several new strategies are likely to be useful. The first is evaluating the range of microclimatic conditions currently present in the Willamette and assessing the extent to which current oak woodlands span this range. Protecting, or at a minimum preventing the loss of, woodlands across the spectrum of local microclimates provides a hedge against future climate changes. The second is the development of a forest genetics management plan. While climate projections for the Valley are within the range experienced by *Q. garryana* throughout its current range, individual oak populations are likely adapted to local climatic conditions. Consequently, it may be beneficial or even necessary to facilitate the "migration" of "pre-adapted" seeds from southerly oak populations (Davis and Shaw, 2001).

Preparedness strategies:

- Monitor and manage conifer (particularly *P. menziesii*) growth and reproduction: current issue, likely to remain relevant, could get slightly better or worse. **High priority.**

- Develop a forest genetics management plan. **High priority.**
- Develop a plan for wildfire management: Wildfires are projected to increase in frequency and intensity. **High priority.**
- Assess the microclimatic variability of current of *Q. garryana* woodlands. Ensure protection (or at a minimum avoid conversion) of woodlands across a wide range of microclimates to hedge against precipitation changes in either direction. **Moderate priority.**
- Monitor and manage deer population/herbivory: Highly uncertain, warmer temperatures could increase winter survival and increase mule deer population leading to more herbivory. **Low priority.**
- Monitor and manage disease/insect pests: Highly uncertain, some suggestions that warmer temperatures will increase insect outbreaks and disease, but no specific data for this system. **Low priority.**

Resource Response Scenario: Expansion

Over the past 100 years, land conversion to development and agriculture combined with *P. menziesii* encroachment has reduced the extent of oak woodlands to a fraction of their historical range (Larsen and Morgan, 1998). In this scenario, warmer and drier summers improve condition for this species in the Willamette Valley and even in some lower elevation areas adjacent to the Valley. *P. menziesii* begins to die back due to increased summer drought or insect pest outbreaks and floodplain agriculture becomes less productive. In this scenario, managers may be able to facilitate transformation to *Q. garryana* and prairie systems (Bachelet et al., 2011). It should be highly feasible to expand oak woodlands occupying the ecotone between conifer and grassland as the conifer dies back. In fact, this transition may happen with little to no intervention. More difficult, but still possible, is the conversion of marginal agricultural lands to prairie or oak systems (Bachelet et al., 2011). However, it is important to keep in mind that as timber and agricultural lands become less economically productive, residential and commercial development becomes an attractive alternative land use. Existing planning policies in the Willamette limit rural development, but declining revenue from timber or agriculture may increase pressure to change those policies. Finding ways to mitigate these lost revenues may be critical to allowing oak expansion to take place.

Preparedness strategies:

- Develop land use policies and conservation practices that support additional protection, conservation and restoration of native habitats. *Q. garryana* woodlands and prairies provide a range of important ecosystem services. Additional conservation areas are needed, and these may be acquired through traditional land acquisition funding sources and techniques (e.g., Land and Water Conservation Funds for expanded or new National Wildlife Refuges, accompanied by the Payment in Lieu of Taxes to Counties program). A payment for ecosystem services program may ease the economic impact of loss of timber or agricultural productivity for private landowners (Bachelet et al., 2011). Another alternative is a transfer of development rights program or cluster development policy can generate income from development for landowners while also protecting native habitats. **High priority.**
- Continue research on restoration techniques to transform former agricultural lands to oak woodlands and prairies. **High priority.**

- Develop criteria for identifying areas for expansion of additional conservation and restoration areas. Think through how these criteria would change under different climate scenarios. **Moderate to High priority.**
- *Q. garryana* is likely to be significantly limited by dispersal capacity. If expansion into previously unoccupied areas upslope becomes attractive (e.g. to replace receding *P. menziesii* forest), assisted migration (i.e., afforestation and reforestation) may be necessary to get oaks to these areas. Under what conditions would this strategy be acceptable? What types of policies or constraints would be needed to implement this strategy? **Moderate to Low priority.**

Resource Response Scenario: Contraction

While climate conditions are likely to remain within the range tolerated by *Q. garryana*, ecological factors both known and unknown could make the Valley, or at least particular sites within it, unsuitable for this species. In this scenario, precipitation does not decrease enough in summer to offset the increases in water-use efficiency of conifers due to CO_2 fertilization. Conifers encroach rapidly on grasslands and oak woodlands. Increased precipitation also favors the growth of a fungal disease that reduces acorn viability. Oak woodlands decline in the Valley and remain in very few sites. The case that *Q. garryana* populations in the Valley decline, the following strategies may become relevant.

Preparedness strategies:

- Monitor oak regeneration, identify competing species which may become dominant, identify cause of oak decline. **High priority.**

- Identify the most climate-resilient sites and focus land use policies and conservation practices that support additional protection and restoration of these high priority areas. (See for example, Michael Schindel, Shonene Scott, and Aaron Jones, The Nature Conservancy, 2013, Rogue Basin Oak Mapping and Climate Resilience, Report to the Medford District, BLM) **High priority.**
- Identify a desirable, and feasible, alternative habitat state, this depends on the source of oak decline. Use management to facilitate conversion to this alternative or at least avoid undesirable conditions. **Low priority.**
- Identify alternative locations for oak establishment, again dependent on the source of oak decline. **Low priority.** For example:
    - CO_2 fertilization advantage to *P. menziesii* – possibly much drier locations could still confer a competitive advantage to *Q. garryana*.
    - Disease outbreak – dependent on disease ecology.
    - Increased summer precipitation favors *P. menziesii* – locate dry "climate refuges"
- Discuss and plan for assisted migration if desired. **Low priority.**

CONCLUSIONS

The case study of *Q. garryana* in the Willamette Valley illustrates the uncertainty and challenges inherent in conducting climate vulnerability assessments even with the best and most sophisticated models available. In this case, multiple lines of evidence paint an optimistic picture of the future of this species in the Willamette Valley. General agreement among a range of climate change and climatic niche model projections provides some confidence that climate conditions in the Willamette will remain within the range currently tolerated by *Q. garryana*.

Increased summer drought may even enhance *Q. garryana's* competitive advantage over conifer species. In addition, there are no presently identifiable negative impacts to important associated species such as seed dispersers, disease or insect pests. Finally, although both mechanistic and climatic niche models project vegetation changes in forest type under virtually all climate scenarios, all of the projected future vegetation types are present within *Q. garryana's* current range. If oaks are currently present in these communities, these vegetation types are likely to be to support this species.

Despite these generally optimistic results, numerous challenges and uncertainties remain in projecting the future of this species. While there is good qualitative agreement among climate change projections for the Willamette, there is significant variation in projected changes depending on the climate variable and season (i.e. mean annual precipitation change ranging from a 9% loss to a 16% gain). The effects of these changes on forest community remain highly uncertain. Mechanistic models project forest to dominate the Willamette, rather than grasslands, suggesting that projected hotter and drier conditions may not be as advantageous to *Q. garryana* as would be expected based on natural history and paleoecological records. Instead, CO_2 fertilization may increase the drought tolerance of competitor species like *P. menziesii*. Variability in climate projections translates into drastically different projections of vegetation change even when using the same vegetation model (i.e. conversion to eastside Cascade forest versus California mixed forest) (Rogers et al., 2011). Reviewing projections from multiple vegetation models and climate scenarios indicates that changes to the general forest type in the Willamette are likely but the forest type projected varies widely depending on the model and climate scenario used.

Finally, models are still limited by the scale at which they can be applied and the number and complexity of factors that can be included. The resolution of even downscaled climate data remains coarse (~1-kilometer) for understanding vegetation change and making management decisions. These broad-scale models are not able to capture fine-scaled processes such as extreme weather events or variation in competition due to fine-scaled topographic and edaphic conditions. Chance events such as the introduction of a new disease or pest could increase oak mortality. The introduction or spread of invasive grassland species could lead to more intense wildfires also increasing adult oak mortality. Urban or agricultural development is likely to limit dispersal to climate refuge locations without management intervention.

Several important technical challenges remain as well. The first challenge is that independent modeling efforts use different climate scenarios. Because the climate scenario used has a significant impact on projected ecological response, it is unclear whether differences in projected vegetation change are due to climate scenario, the ecological response model used, or both. Understanding which specific factors within each climate scenario lead to the projected ecological responses would help identify possible trends in ecological response (i.e. climate scenarios with more winter precipitation favor conifer growth while drier models favor chaparral). However, such details are not always included in publications. Secondly, comparing projected vegetation types between modeling efforts is extremely challenging because each modeling effort uses a unique vegetation classification system.

Reviewing multiple information resources for this case study both increased confidence in particular outcomes, such as the broad-scale continued climatic suitability of the Willamette Valley for *Q. garryana*, and highlighted significant uncertainty, for example in how the vegetation community may change. Developing a conceptual model of factors influencing oak viability facilitated reviewing potential changes to associated species such as seed-dispersing animals and herbivores. Finally, resource response scenarios provided several important benefits to adaptation planning. Developing scenarios allowed the planning process to incorporate and acknowledge uncertainty and variability in ecological response projections explicitly. Especially in a case such as this one where qualitative agreement is comparatively strong, developing a wide range of plausible resource response outcomes forces managers to consider alternative possibilities and avoid focusing solely on the most likely outcome. This facilitated the identification of a wide range of management strategies. Identifying strategies targeted to individual scenarios was more feasible than trying to address the full range of possible future changes simultaneously. Overall, the combination of reviewing a wide range of information resources coupled with the development of resource response scenarios was an effective strategy for building understanding of potential future changes and defining and incorporating uncertainty without paralyzing the planning process.

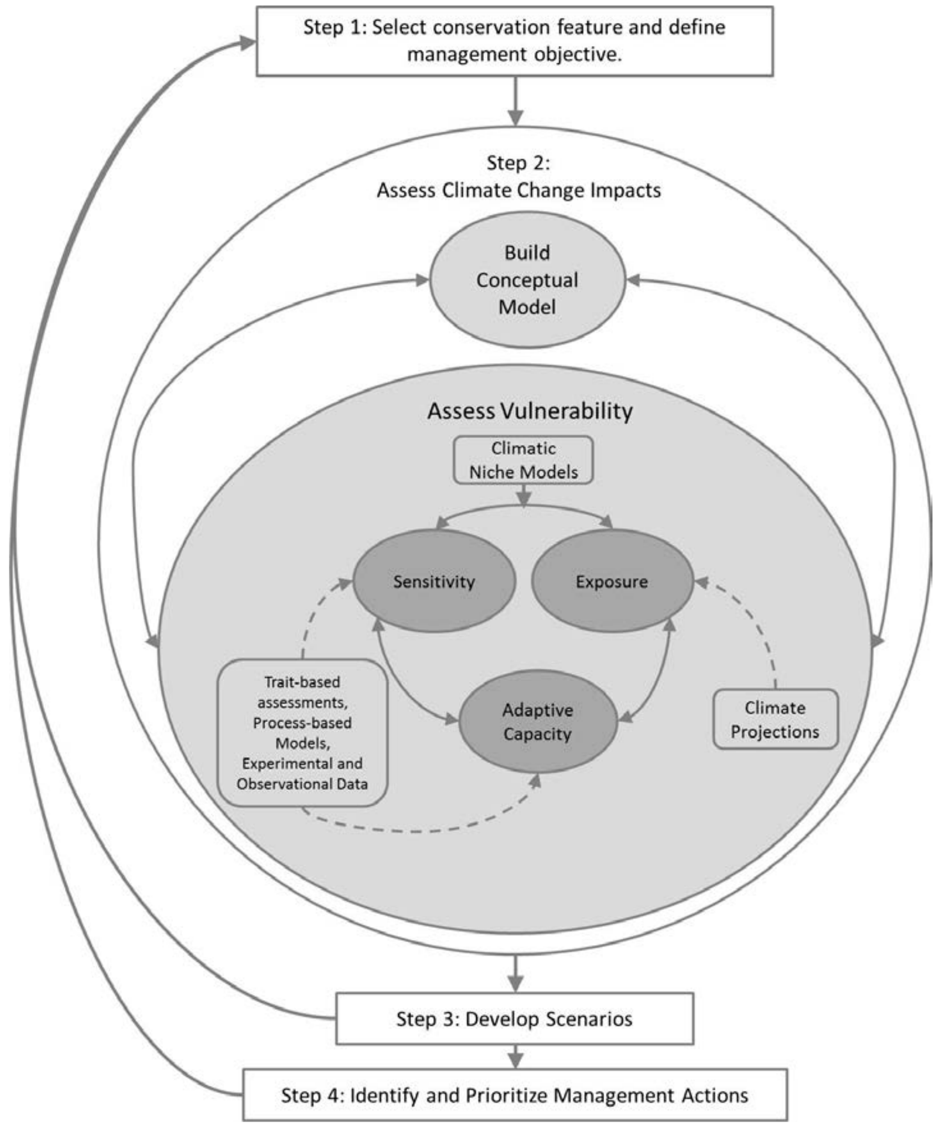

Figure 3.1. A modified version of the framework for climate adaptation planning from Cross et al. (2012) including vulnerability assessment. Types of data that support each element of the vulnerability assessment are shown in boxes with rounded edges and are based on recommendations from Dawson et al. (2011).

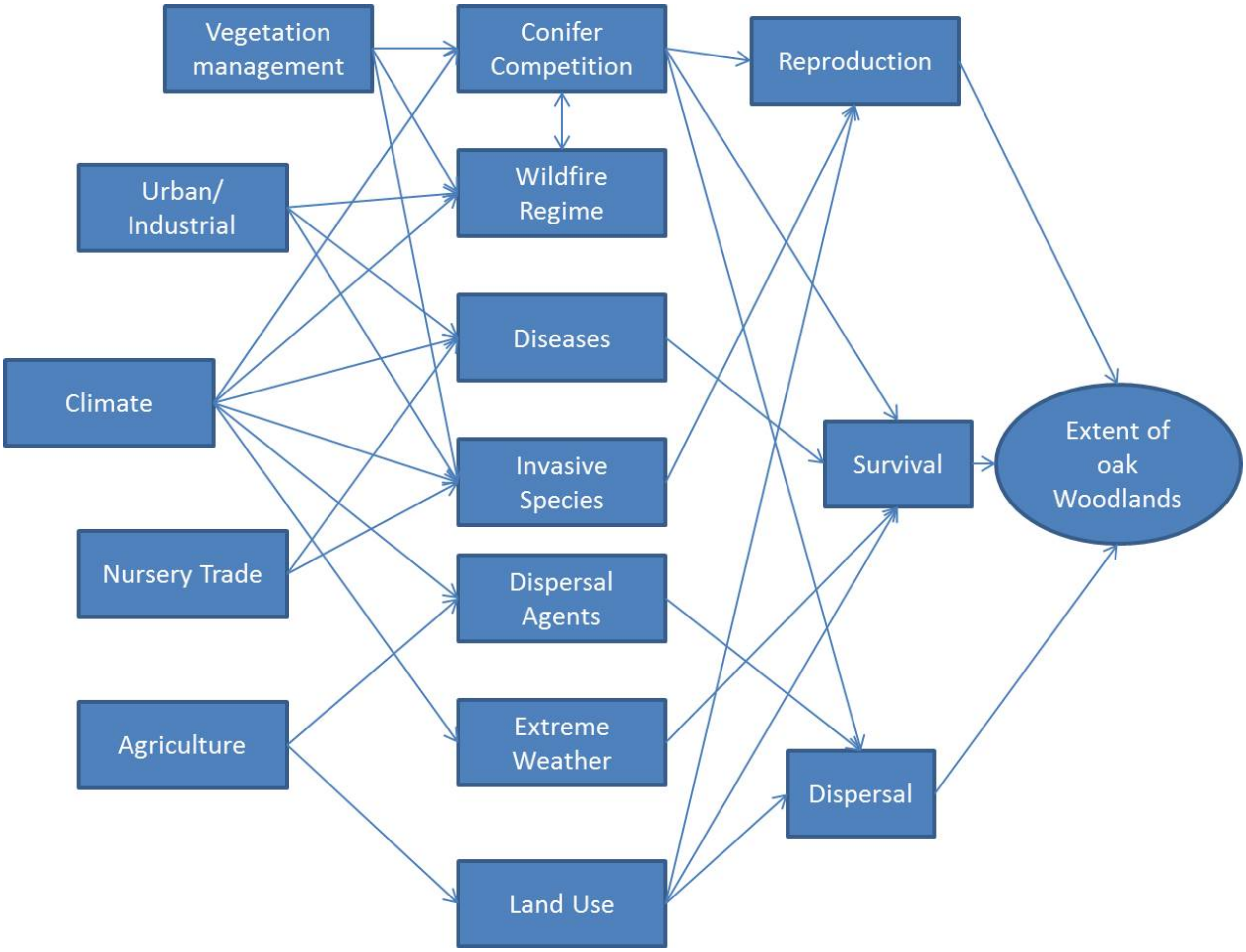

Figure 3.2. Conceptual model of the critical drivers of *Q. garryana* extent. This model was used to structure the assessment of climate vulnerability presented here.

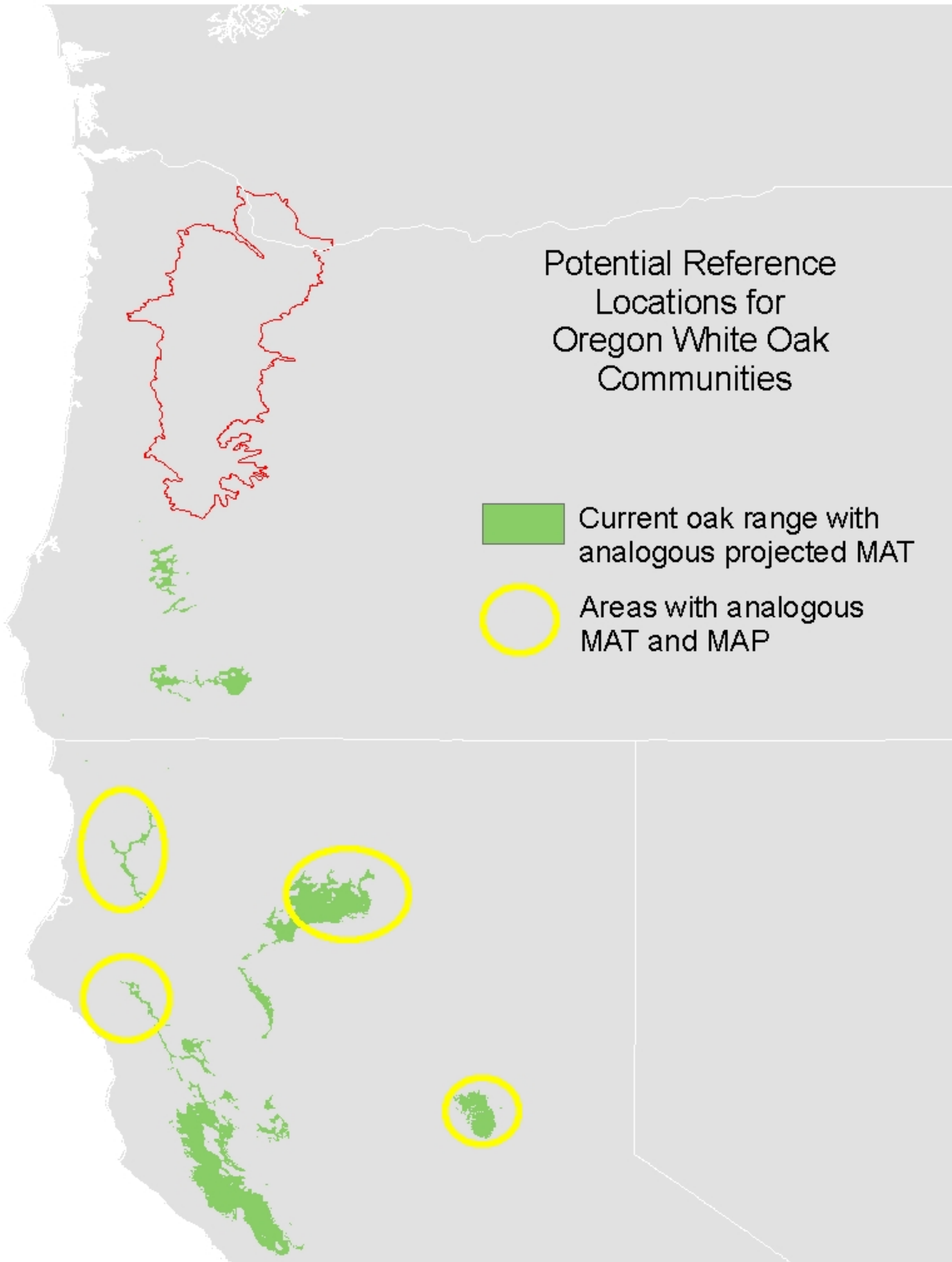

Figure 3.3. Areas within *Q. garryana's* current range (green) that currently have a mean annual temperature (MAT) similar to that projected for the Willamette Valley by 2100. Areas circled in yellow also have similar mean annual precipitation (MAP).

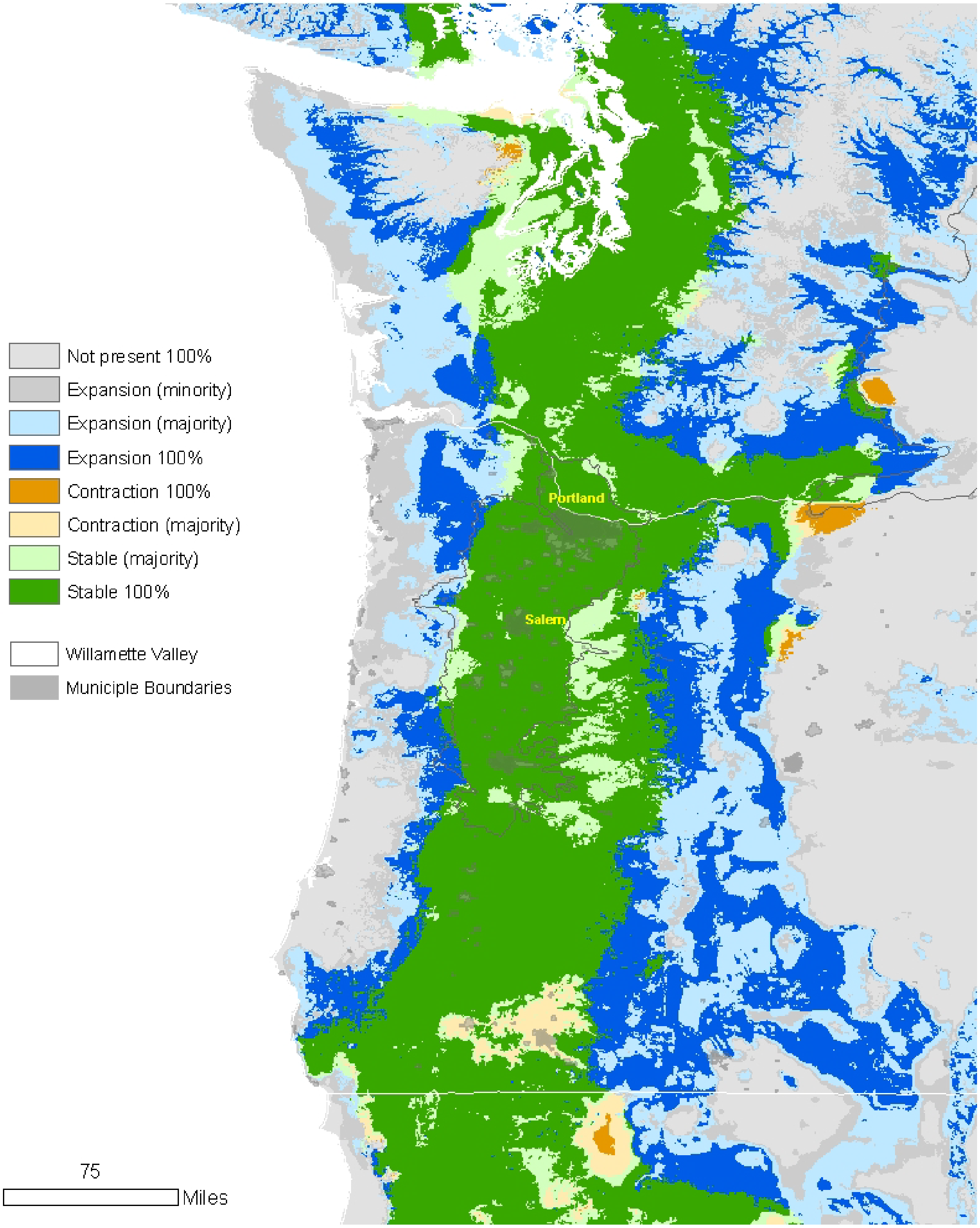

Figure 3.4. Climatic niche model results for *Q. garryana* using five climate scenarios (BCCR BCM 2.0, CCCMA CGCM 3.1, CSIRO MK 3.0, INMCM 3.0, MIROC 3.2 (Medres)) all based on the A2 emissions scenario for the 2080s (data developed by Case and Lawler, 2012). Majority agreement means that projections from three or more climate scenarios agree.

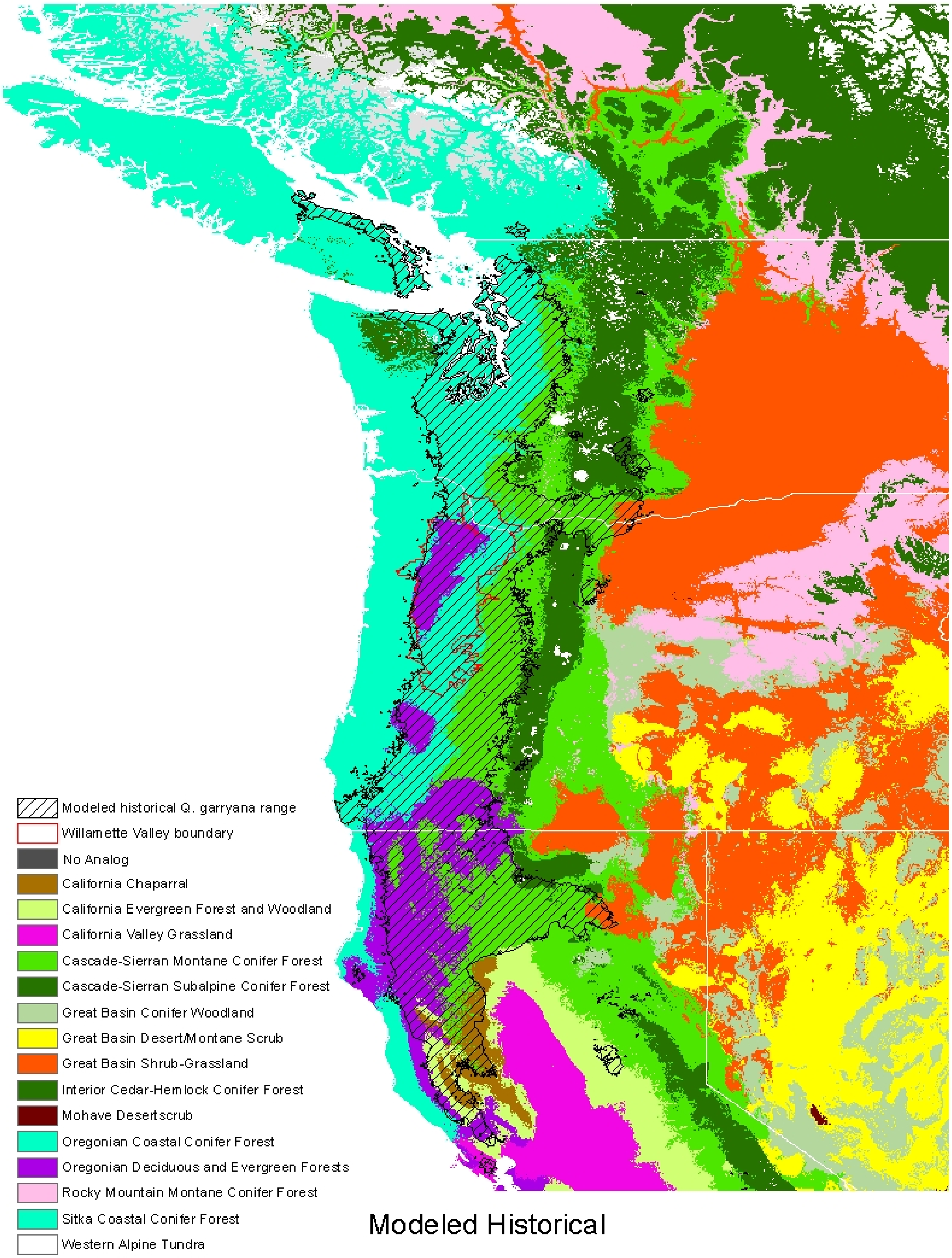

Figure 3.5. Modeled historical vegetation biomes (data provided by Rehfeldt et al. 2012) and modeled historical *Q. garryana* range (data provided by Case and Lawler, 2012).

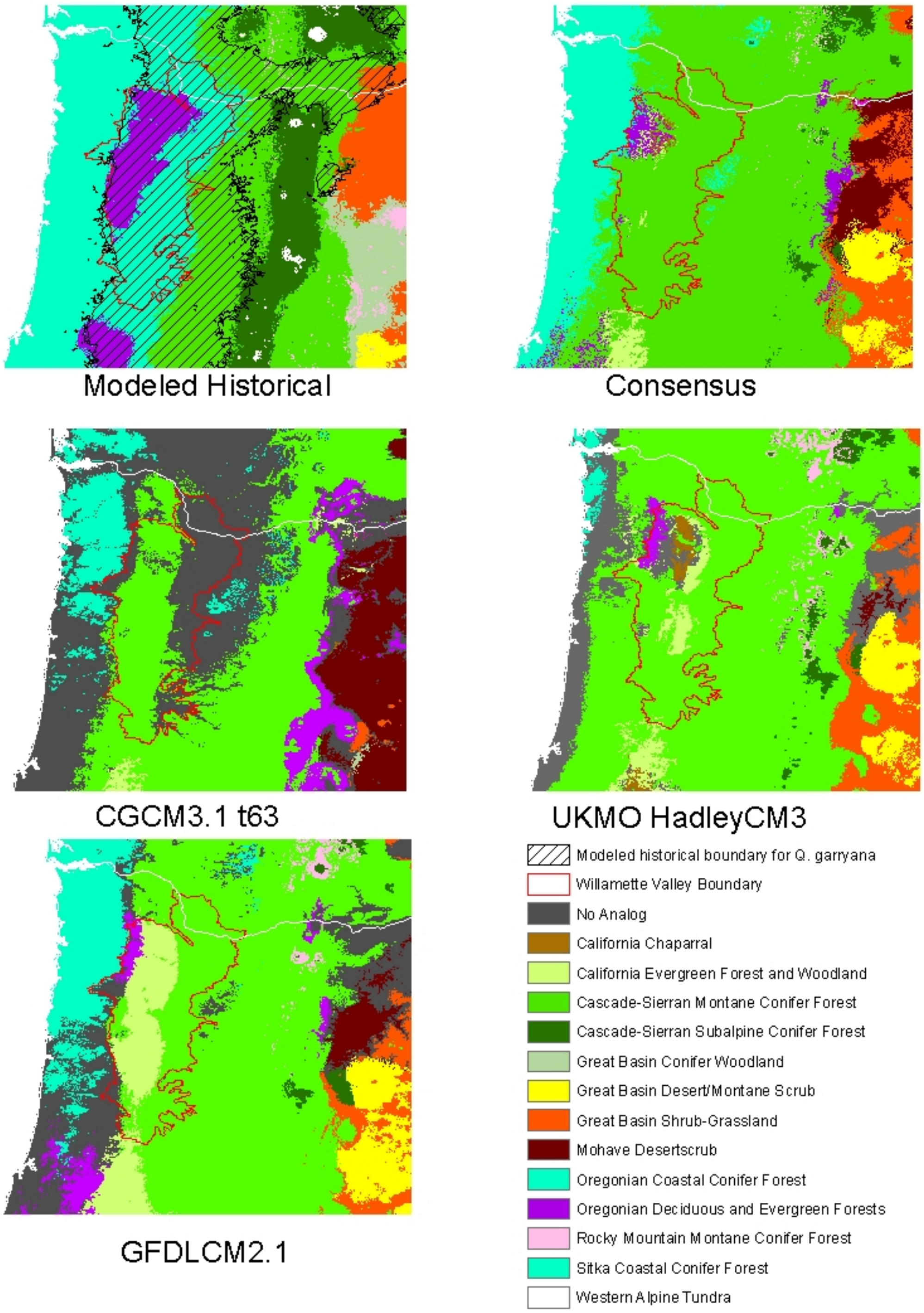

Figure 3.6. Projected historical (a) and future (b-e) vegetation biomes using a climatic niche model for the decades surrounding 2090 (data provided by Rehfeldt et al. 2012). The Willamette Valley ecoregion is outlined in red. Map (a) shows modeled historical vegetation with modeled historical *Q. garryana* range provided by Case and Lawler (2012) overlaid (hatched). The consensus map (b) shows the vegetation type projected by the majority of six climate scenarios (three GCM models x two emissions scenarios each) ignoring no-analog projections. Maps c-e show projected vegetation for individual GCM models all using the A2 emissions scenario. No-analog climates are shown in dark gray.

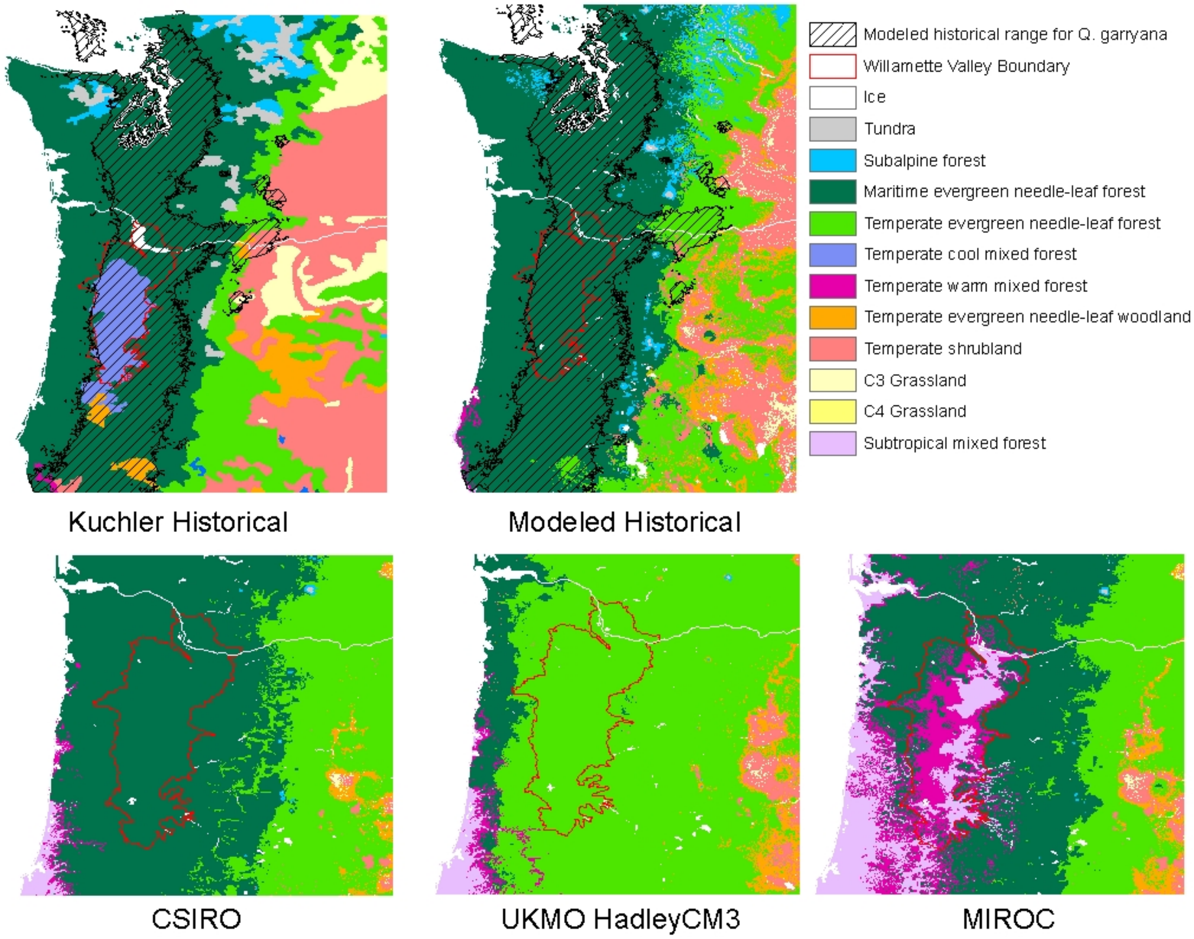

Figure 3.7. Projected vegetation types using the MC1 DGVM with full fire (i.e. no fire suppression) (data presented are provided by Rogers et al. 2011). Shown are the most common vegetation types for the historical (1971-2000) and future (2070-2099) periods under the three climate projections: the CSIRO Mk3 [Gordon, 2002], MIROC 3.2 medres [Hasumi and Emori, 2004], and Hadley CM3 [Johns et al. 2003] models run through the A2 CO2 emissions scenario (Nakicenovic and Swart, 2000). Also shown is the aggregated potential vegetation map from Küchler [1975]. Notice that the unique Willamette vegetation type illustrated in the Küchler map is absent in the MC1 historical projection.

Table 3.1. shows projected climate changes for the A2 ensemble mean and the maximum and minimum values projected by any of the 10 model projections (5 models x 2 emissions scenarios). Changes are calculated as difference between 30 year averages for the end of the century (2070-2099) and the 30 year historical period (1961 - 1990) and represent the average change for the Willamette Valley region.

	A2 Mean	Min	Max
Mean Annual Temp (°F) (Increase, °F)	58 (6.2)	54 (2.7)	59 (7.9)
Spring Mean Max Temp (°F) (Increase, °F)	56 (4.8)	52 (0.9)	57 (5.2)
Summer Mean Max Temp (°F) (Increase, °F)	74 (8.6)	71 (5.2)	78 (12.0)
Max mean temp for the warmest month (°F) (Increase, °F)	78 (10.1)	74 (5.9)	83 (15.3)
Min mean temp for the coldest month (°F) (Increase, °F)	45 (5.0)	42 (2.5)	47 (4.3)
Mean Annual PPT Change (%)	3	-9	16
Winter PPT Change (%)	5	-11	21
Spring PPT Change (%)	1	-8	17
Summer PPT Change (%)	-36	-52	-14
Autumn PPT Change (%)	12	-11	14
Precipitation as Snow (SWE) Change (%)	-87	-100	-11
Spring PET Change (%)	-16	-26	-10
Summer PET Change (%)	1	-17	17
Number of Frost Free Days	365	363	365
Growing Degree Days with base 0 Change (%)	31	13	39

PPT = Precipitation
PET = Potential Evapotranspiration

RESEARCH SUMMARY AND FUTURE DIRECTIONS

Urbanization and climate change represent two of the greatest challenges to ecological planning and biodiversity conservation. Meeting these challenges requires that as ecologists and planners, we improve our understanding of the complexity of ecological response to change. In my dissertation, I sought to contribute to this need in two ways. First, by contributing to our understanding of how ecosystems respond to land-cover change though an empirical study of the effects of landscape structure on Oregon white oak (*Q. garryana*) regeneration patterns and processes. Second, I developed and illustrated an approach to incorporating uncertainty into climate vulnerability and adaptation planning using *Q. garryana* in the Willamette Valley as a case study. These two studies explore the interactions between landscape structure and management, biodiversity change, and ecosystem function and response. Using *Q. garryana* as a focal species throughout allowed me to explore this complex system at two very different spatial and temporal scales. In this section, I review the contributions of my research to three areas: urban ecology, *Q. garryana* management, and ecological planning. I end with a discussion of the implications of this work for ecological planning and directions for future research.

Contributions to Urban Ecology

Seed dispersal is a critical driver of forest biodiversity (Howe and Miriti, 2000; Janzen, 1970; Levin et al., 2003). Anthropogenic changes to landscape structure and forest biodiversity can lead to dramatic reductions in seed dispersal services (Caves et al., 2013; Markl et al., 2012; McConkey et al., 2012). Numerous studies have documented changes to seed dispersal patterns following habitat fragmentation, but these have been conducted almost entirely in agricultural or otherwise rural landscapes (Breitbach et al., 2010; Christian, 2001; Garcia et al., 2010;

McConkey et al., 2012; Moran et al., 2009). Urbanization may have a particularly significant impact on seed animal-mediated dispersal because animal species assemblages and habitat structures are highly altered in urban landscapes (Blair, 1996; Donnelly and Marzluff, 2004; McDonald et al., 2013; McKinney, 2008). The composition of biodiversity within a landscape or ecosystem has a critical impact on ecological function (Hooper et al., 2005). While biodiversity *per se* is an important property to measure and protect in ecological systems, those species that control resources or provide a vital ecosystem service have a disproportionate impact on ecosystem function (Walker, 1995). Seed-dispersing animals play a critical ecological role in maintaining biodiversity and forest function in fragmented landscapes (Farwig et al., 2006; McConkey et al., 2012). In urban landscapes, habitat fragmentation and isolation are key drivers of ecological degradation (Crooks et al., 2004; Lundberg et al., 2008). As a result, protecting animals that provide dispersal services, or so-called "mobile-link" species is particularly critical for urban forest function (Lundberg and Moberg, 2003). In addition, protecting animal species that provide seed dispersal services has significant economic value for urban park management (Hougner et al., 2006). Despite the importance of seed dispersal to forest function generally and urban forests in particular, little is known about how urbanization influences seed dispersal services, and what the subsequent consequences may be for urban forest regeneration. My research contributes to this knowledge gap by directly comparing seed dispersal services in urban and non-urban oak woodlands. I measured dispersal services directly by tracking individual acorns as they moved through the landscape. In addition, I used experimental acorn plantings and measured seedling and sapling abundance to track whether dispersal patterns ultimately impact oak regeneration.

My findings of higher acorn removal in urban compared to non-urban landscapes contrast with previous studies of the effects of fragmentation on seed removal. Seed removal, or the number of fruits removed from a tree or plant, is often used to measure dispersal activity (Carlo and Morales, 2008). Higher removal is generally considered to indicate more effective dispersal services, although this is clearly not always the case (see Chapter 2). The majority of previous studies, conducted in fragmented agricultural or rural landscapes, found that fragmentation led to the loss of seed-dispersing animal species in forest fragments and subsequently a reduction in seed removal, often with measurable negative consequences for forest seedling diversity (Cordeiro and Howe, 2003; Kirika et al., 2008; McConkey et al., 2012). However, a few exceptions to this trend exist. Farwig et al. (2006) found increased avian visitation to and fruit removal from *Prunus africana* trees in forest fragmented and degraded by agriculture compared to low disturbance sites. The authors suggested that fewer fruit resources may be available in degraded forest fragments, making *P. africana* fruits particularly attractive in these areas. Similarly, Breitbach et al. (2010) found that the diversity and abundance of seed dispersing bird species decreased along a gradient of increasing agricultural intensity. However, plant visitation and fruit removal remained constant suggesting that birds traveled longer distances in intensely agricultural landscapes to reach these desirable fruit resources. Thus, due to behavioral adaptation of birds, seed dispersal services were maintained in this highly altered landscape.

These contrasting studies indicate that animal-mediated seed dispersal may be resilient to forest fragmentation under certain circumstances. In urban oak woodlands, the chance introduction of eastern gray squirrels to the west coast of North America facilitated the presence of a disturbance tolerant seed-disperser for oak acorns. In addition, native Steller's jays are highly mobile and able to colonize urban landscapes (Vigallon and Marzluff, 2005). Urban oak woodlands therefore meet the first requirement for seed dispersal resilience of having mobile, disturbance-tolerant animal species available to provide dispersal services.

However, characteristics of urban oak ecosystems suggest that the dynamics leading to higher acorn removal differ from those driving removal dynamics in agricultural landscapes. In contrast to the suggestions by Breitbach et al. and Farwig et al. that landscape-level fruit scarcity leads to high visitation and removal rates in agricultural landscapes, my findings of increased acorn removal combined with decreased dispersal distances suggest that food resource scarcity is not driving these dynamics. Instead, urban landscapes are likely supporting high densities of a few species, such as eastern gray squirrels (Shochat et al., 2010). Higher densities lead to a more competitive foraging environment, which can explain my observations of both increased removal and shorter dispersal distances (Hopewell et al., 2008).

The mechanisms driving higher densities in urban environments remain uncertain, but potentially result from the combined reduction in top-down predation pressure and bottom-up increase in resource availability in urban environments (Shochat et al., 2010). Eastern gray squirrels may be particularly well suited to urban landscapes because they are able to compact their home range size and subsequently exist at high densities in small forest fragments (Koprowski, 2005). Potential explanations include higher nut resource availability along forest edges, although this theory has not been tested. The relationship between fragmentation and squirrel densities is particularly complex in urban landscapes. A study of urban squirrels in forested parks in the Washington D.C.-Baltimore region found no relationship between squirrel density and habitat suitability based on forest patch characteristics within urban parks. Instead, the authors found a negative relationship between squirrel density and availability of food and nesting resources in the urban matrix adjacent to parks (Parker and Nilon, 2012). In other words, as the quality of squirrel habitat in the urban matrix surrounding forested parks improved, effectively expanding habitat beyond park boundaries into the surrounding urban matrix, squirrel densities declined. Urban parks set in intensively urbanized regions with little tree cover support extremely high densities of squirrels likely due to both small habitat patch size and the availability of supplemental food of anthropogenic origin (Parker and Nilon, 2008, 2012).

The potential influence of urban matrix conditions on squirrel densities has important implications for urban landscape management. While the presence of eastern gray squirrels in urban oak woodlands is beneficial for providing acorn-dispersal services, high densities of individuals are likely detrimental to oak acorn dispersal. This is because although more acorns were handled (removed) in urban landscapes, these acorns also had a higher probability of being consumed rather than cached and were dispersed shorter distances (Chapter 2). Park managers and urban residents may be able to decrease squirrel densities, and therefore improve dispersal services in urban oak woodlands, by improving the quality of squirrel habitat in the urban matrix surrounding forest parks. Specifically, a more forested (i.e. more trees, more tree canopy cover and less building cover) urban matrix may allow urban squirrels to expand their territories as they would in un-fragmented landscapes resulting in lower densities of squirrels in urban parks. Such management actions may have significant implications for urban forest dispersal and regeneration processes.

While urban development has measurable, negative impacts on dispersal, the overall implications of urban development for oak regeneration are complex. Germination and seedling production were not significantly different in urban versus non-urban oak woodlands (Chapter 2). Similarly, seedling abundance was not correlated to the amount of urban development surrounding oak woodlands (Chapter 1). These results suggest that despite higher acorn predation rates and shorter dispersal distances, *Q. garryana* in urban landscapes are equally capable of producing seedlings, given the opportunity (i.e. suitable understory conditions). This apparent contradiction may be due to temporal variability in acorn production (i.e. acorn masting). In mast years, high acorn production may successfully overwhelm even the high acorn predation rates observed in urban landscapes, making oak reproduction ultimately resilient to these effects at this early stage.

While seedlings are readily produced, young saplings were significantly less abundant in urban compared to non-urban oak stands (Chapter 1). These findings suggest that oak seedling recruitment to the sapling stage may be limited in urban environments. One potential explanation for this is higher grazing pressure in urban landscapes due to a higher density of herbivores such as deer in urban environments (Côté et al., 2004). Alternatively, although only plots with un-managed understory were included in this study, I did observe that otherwise un-managed grassland was mowed one year in one urban park (site 18). Mowing would certainly decrease sapling abundance. Fields of Scotch broom (*Cytisus scoparius (L.) Link*) were mowed occasionally (e.g. once in three years) in both urban and non-urban areas, but saplings were if anything more abundant in areas with Scotch broom (Chapter 1). In general, saplings were more abundant in areas with shrub understory, and these areas were not mowed in either landscape. However, several oak woodlands and individual sites within woodlands were excluded from my sample due to mowing and understory management. Limiting mowing and/or identifying and protecting oak saplings from mowing are two actions managers can take to help facilitate oak regeneration in both urban and non-urban landscapes.

Finally, abundance of larger saplings did not differ depending on the amount of urban development surrounding oak woodlands (Chapter 1). Older saplings were defined as those with a Diameter at Breast Height (DBH) between 2.5 and 10 centimeters. One survey of *Q. garryana* stand structure found that even saplings with a DBH of only 10 centimeters were a minimum of 59 and up to 162 years old (Gilligan and Muir, 2011). Consequently, even saplings < 10 cm should not be considered the products of recent regeneration. Consequently, the larger oak saplings observed in urban environments may have established prior to urbanization in this region. Another possible explanation is that once saplings reach a certain size, survival is higher in urban landscapes. This would mean that although seedling mortality is higher in urban areas, sapling survival is also higher leading to equivalent numbers of larger saplings in urban and non-urban environments.

In summary, forest regeneration processes are composed of multiple stages and each is influenced by different drivers. The urban environment has the potential to influence virtually all stages of regeneration by both altering the animal community that interacts with *Q. garryana*, and the environmental conditions affecting seedling production and survival. Through my research, I found strong evidence that urbanization influences stages of oak regeneration that are controlled by animal species, specifically acorn dispersal and predation. Urbanization may also have an impact on seedling survival and subsequent sapling abundance, although drivers of this pattern remain unclear. This research suggests that the unique structure of urban ecosystems may result in fundamentally different seed dispersal and forest regeneration dynamics from those found in other fragmented systems.

Implications for Oregon White Oak Management

Q. garryana is a priority conservation species throughout its range (Larsen and Morgan, 1998). Conservation of this species and associated prairie systems has inspired the development of the Cascade Prairie Oak Partnership, a regional consortium of researchers, resource managers, and conservation biologists devoted to the conservation and management of this species (http://cascadiaprairieoak.org/home). My research contributes to the conservation and management of this species by clarifying the significance of landscape structure in driving oak regeneration patterns and processes, which has significant implications for landscape management. In addition, my research provides basic descriptive natural history data for both urban and non-urban oak woodlands.

Through my research, I found that vegetation structure, particularly the presence and spatial arrangement of conifer forest, but likely shrub cover as well, has important implications for *Q. garryana* regeneration. These relationships were similar in both urban and non-urban landscapes. Consequently, this finding has implications for restoration and management of this species in both landscape types. Protecting conifer cover adjacent to or within short distances (~ 100 meters) of oak stands may facilitate the spread of acorns away from oak stands. However, conifers compete with *Q. garryana* and so acorns dispersed to these areas may not ultimately recruit to adulthood (Devine and Harrington, 2006). If this is the case, then adjacent conifer forest may in fact represent a sink habitat for these acorns. Nevertheless, maintaining patches of conifer forest in close proximity to oak woodlands will provide important habitat for tree squirrels (Johnston, 2013), which subsequently provide dispersal services. Consequently, when ecological planners have the opportunity to protect *Q. garryana* stands, protecting some of the surrounding landscape, ideally including a mix of conifer forest and grassland, will help provide the habitat requirements to support acorn-dispersing animals as well as provide potential habitat for oak stand expansion.

If oak expansion into non-forested grassland is desired, managers either need to hand disperse acorns to these areas, or experiment with providing structures such as shrub, trees, or perhaps even artificial cover to attract acorn dispersal into these areas. During my transect surveys, I observed seedlings present under lone conifer trees or clumped shrubs in otherwise open grasslands (Chapter 2). The small sample size was not sufficient to test statistically, but anecdotally, the presence of even a few seedlings suggests that these features may facilitate acorn dispersal into non-forested grasslands. Including these features in managed areas may help facilitate dispersal into non-forested grasslands where recruitment may be more likely. If acorns are hand dispersed, planting the acorns beneath the soil surface will be necessary for germination and seedling production to occur effectively (Figure 2.8, Figure 2.10).

Shrub cover also plays a potentially important role in both dispersal and regeneration. Acorn handling was significantly higher in plots with shrub cover compared to those with grass indicating higher levels of foraging in this habitat type (Chapter 2). Previous studies have found higher rodent activity in areas with shrub cover in other oak systems (Munoz and Bonal, 2007, 2007; Smit et al., 2001). Seedling production was not consistently higher in shrub habitats compared to grass habitat, but seedlings were produced in this habitat type (Chapter 2). Overall, seedling abundance was significantly lower in shrub compared to grassland habitats, but saplings were significantly more abundant in shrub understory (Chapter 1). I did not include non-forested shrub plots in my acorn dispersal study, but I suspect that dense shrub cover such as snowberry could also facilitate the spread of acorns out from under existing oak canopy by providing cover for seed-dispersing animals. This is an important area for further research.

In urban landscapes, at a most basic level, urban park managers can provide or maintain some areas where natural regeneration can occur by limiting the amount of manicured lawns in parks with oak stands. Including a mix of grass and shrub (i.e. snowberry) cover may be wise because acorn predation in shrub habitats is high, while seedling survival in grass understory may ultimately be low. In addition, assessing seedling and sapling abundance can help determine the likelihood of new oak recruitment and identify needed management strategies. I found no seedlings present during surveys of two of my urban oak sites, sites 12 and 67 (Figure 2.1). Both sites had very high rates of acorn handling and subsequently predation (Figure 2.6). This suggests that while urban oak seedling production is no different overall, acorn predation in particular areas may be so intense that seeding production is suppressed. In this case, in the short-term, protecting some acorns from predation may be necessary to facilitate regeneration in these areas. In the long-term, protecting and encouraging the establishment of large, nut-bearing trees in urban areas surrounding forest parks may decrease squirrel densities in these areas (Parker and Nilon, 2012). Lower squirrel densities may lead to more beneficial acorn dispersal services if competition subsequently decreases. Surveying sapling abundance is also important for determining the likelihood of seedlings ultimately recruiting to the adult stage. Depending on whether herbivore pressure is truly higher in urban oak stands, protecting some seedlings from herbivory may be a simple and effective method for encouraging oak regeneration.

Contributions to Addressing Uncertainty in Ecological Planning

Planners need the ability to develop flexible and robust management strategies even when information is incomplete and the future is uncertain. My small contribution to this immense challenge was to develop a checklist of questions designed to facilitate reviewing and integrating diverse sources of information that can inform climate vulnerability assessment. Then, to address irreducible uncertainty, I proposed the use of resource response scenarios as a planning method to incorporate uncertainty explicitly and assist in the identification of flexible and robust planning and management strategies. Finally, practical examples of ecological climate adaptation planning are needed because significant technical and intellectual challenges arise when trying to apply climate vulnerability assessments to the management of real landscapes. To illustrate my proposed approach, I provide a case study assessment of climate vulnerability and adaptation strategies for *Q. garryana* in the Willamette Valley.

The checklist presented in Chapter 3 aims to help planners review information relevant for assessing climate vulnerability. The checklist helps managers organize climate impacts into categories of increasing complexity and uncertainty by focusing first on direct climate impacts, then indirect impacts, and finally non-climate stressors. In addition, the checklist is designed to help remind managers of limitations to particular information resources. For example, even downscaled climate and ecological response projections cannot capture fine-scaled interactions and events that may have a significant impact on resource response. In addition, models in general do not capture all relevant drivers of system behavior and including even a qualitative assessment of these factors can help highlight uncertainty and knowledge gaps.

Including a wide range of climate and resource response projections was important for evaluating climate vulnerability in *Q. garryana* in the Willamette Valley. Specifically, reviewing multiple sources of information helped generate confidence in some projections, such as the expected continued suitability of climatic conditions for this species in the Valley. This review also highlighted significant uncertainties, for example in how the general forest type dominating the Valley will change. Uncertainty as to how vegetation cover will change stemmed both from uncertainty in how the climate will change (i.e. variability in model projections using the same vegetation model but different climate scenarios) and uncertainty in how vegetation will respond to climate change (i.e. variability in model projections using the same climate scenario, but different vegetation response models). Incorporating natural history information helped identify potential impacts from factors not included in any of the resource response models such as disease, herbivory, and dispersal services. In short, the use of a range of information resources for addressing climate vulnerability helped to identify consensus, important areas of disagreement, and knowledge gaps in expected climate change impacts.

Resource response scenarios provided a useful framework for incorporating uncertainties identified during the vulnerability assessment process. A focus on climate scenarios alone can challenge adaptation planning because ecological response to climate change is so uncertain. Scenarios can allow managers to use the variability in expected resource response productively to create more effective adaptation plans. Uncertainty often stymies the planning process as managers wait for more information, assuming that eventually more research will lead to greater consensus about future changes. However, such consensus is unlikely given the complexity of both climate and ecological systems and the scale and extent of expected changes (Maslin and Austin, 2012). Instead, managers will need to move forward with planning and action despite these uncertainties (Millar et al., 2007; Stein et al., 2013). Scenarios can help re-orient managers away from trying to identify the most likely future and instead help them develop strategies to meet their management goal under a wide variety of future conditions.

Implications for Ecological Planning and Future Research Directions

Both climate and land-cover change have and will continue to have dramatic impacts on biodiversity in the coming decades. These changes have significant implications for biodiversity conservation approaches and goals at the most fundamental levels. Stemming the tide of current biodiversity loss requires that planners can develop ecological networks that can help support biodiversity and protect ecosystem functions despite landscape and climate changes. The prevalence of human-dominated landscapes means that such areas must be part of this solution. Finally, these combined changes challenge our current ability to define and maintain ecosystems within the range of historical variability. As a society, we will need to grapple with our goals for the planning and management of ecological systems and our definitions of success.

Urban ecology research is building a more complete and detailed understanding of how urbanization influences landscape structure, biodiversity and ecosystem services (McDonald et al., 2013). In particular, we are starting to develop a more mechanistic understanding of why urban landscapes support a small number species at very high densities (e.g. Shochat et al., 2010). Yet we are still a long ways from developing planning and management actions that can reverse this trend. To improve the capacity of urban landscapes to support plant and animal species that we value, we must understand the factors that drive these changes in biodiversity pattern, and identify potential management actions that can reverse negative trends.

In my research, I found that higher densities of squirrels in urban areas likely have a negative effect on oak acorn dispersal. This finding indicates that not only does the trend towards reduced species diversity and evenness negatively affect biodiversity measures, but also it has negative implications for urban ecosystem function. In my research, I used simple definitions and measures of the "urban" environment. The goal of this present study was to identify whether differences in seed dispersal processes exist between urban and non-urban sites. In future extensions of this research, I hope to add more complex measures of the urban matrix such as development age, building and population density, and quality and extent of forest cover to gain a more mechanistic understanding of how specific features of the urban environment may affect urban seed dispersal dynamics. These particular features may influence urban squirrel densities (Parker and Nilon, 2012), with important implications for forest function. In addition, I would like to expand the spatial scope of my seed dispersal study to include a wider range of landscape types including a gradient of urban intensity and, possibly, agricultural landscapes. Measuring dispersal and regeneration functions across a gradient of urbanization could identify if there is a threshold or non-linear response to changes in dispersal functions with increasing urban intensity. Comparing urban and agricultural landscapes would be useful for distinguishing between the effects of fragmentation and the effects of the urban matrix.

More and better empirical data on how ecosystems respond to dramatic changes in species assemblage is essential for effective ecological planning and management. However, the complexity of ecological systems challenges our ability to predict these responses with the level of specificity needed to make management decisions. Consequently, managers need planning approaches that use uncertainty as an asset rather than a roadblock to planning. Developing a range of plausible scenarios of future resource condition is one potential approach. However, while scenarios are often touted as an effective planning tool, they are still rarely applied in ecological management. We have much still to learn about how to develop and effectively use scenarios. What factors need to be included for scenarios to be most effective? My example scenarios are very simply constructed and focus on ecological changes almost exclusively. For my goal of identifying a first cut of possible planning and management actions, this was effective. However, it would be useful to add additional drivers, particularly socio-economic and cultural, to the scenarios and see whether and how this added complexity leads to the development of new or different adaptation strategies or priorities.

Incorporating uncertainty into spatial ecological planning is an important next step in adaptation planning. Land use decisions are often irreversible. In light of projected changes, land protection efforts will need to be resilient or robust to future changes. Simultaneously, we will need to develop protection strategies that are more flexible and reversible. Incorporating climate change dynamics into spatial planning is one of the most significant challenges ahead for ecological planners. I believe that scenarios could be useful in this effort as well if they are used to identify lands that are a priority based on a variety of plausible scenarios of ecological response to climate changes.

Finally, the degree of ecological transformation expected, due to land-cover and climate change, challenges traditional measures of ecological management success. Much of ecological planning is focused on recreating the past, but planners will now need to look to the future (Stein et al., 2013). Changing management objectives from maintaining past conditions to anticipating the future will not be easy. In a review of climate adaptation plans developed by conservation managers at The Nature Conservancy, Poiani et al. (2011) found that 52% of the plans focused on resistance strategies. That is, strategies that strive to maintain current biodiversity and ecosystem structure as is as the climate changes. Only two plans included transformation strategies. In contrast, the ecological literature unequivocally states that ecological transformations will be common and managers will need to develop strategies to facilitate this process (Grimm et al., 2013; Stein et al., 2013). Without the benefit of using the past as guidance for the future, it will be difficult to judge which species, functions, and processes we should prioritize, protect and encourage, and when our resistance actions are “ossifying” the system, possibly pushing it towards collapse. As human-dominated landscapes expand and climate changes intensify, the pace and scale of ecological change will increase. In some cases, these changes may be relatively minor, such as a subtle decrease in seed dispersal services. However, in many cases the changes will be dramatic shifts to new vegetation regimes (Gonzalez et al., 2010) or novel ecosystems (Hobbs et al., 2006). In such cases, we will need to reevaluate our definition of a desirable ecosystem state (Hobbs and Cramer, 2008). Ecological planning goals will need to evolve as conditions change and our understanding of ecological resilience and transformation matures (Stein et al., 2013). Building an understanding of how human-dominated ecosystems function and the feedbacks between human and biophysical components will be essential not only to understanding the "how" but also to identifying and articulating the "why" of ecological management in the face of this rapid environmental change.

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Supplementary Table 1: Distribution of plots within sites. Sites 12-90 are urban and sites 189-298 are non-urban (see Figure 1 for a map of the study area). Numbers in parentheses indicate where plots were removed from the final sample because canopy cover measurements did not fit the definition for the study. 2009 was a pilot year and so plots were only located at two sites, 90 and 252. In 2011, plots were placed in the same (if all acorns from 2010 were removed) or within 5 meters of the 2010 location.

			Non-forest Grassland			Conifer/Open-Herb			Conifer/Shrub			Oak/Grassland			Oak/Shrub		
Site	n (original)	n (with plots removed)	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011	2009	2010	2011
12	8	8	0	0	0	0	2	2	0	1	1	0	0	0	0	1	1
18	16	16	0	2	2	0	2	2	0	0	0	0	2	2	0	2	2
67	12	12	0	2	2	0	0	0	0	1	1	0	0	0	0	3	3
75	8	8	0	1	1	0	1	1	0	1	1	0	1	1	0	0	0
90	27	26	3	1	1	5	1	1	1 (-1)	1	1	2	2	2	4	1	1
189	8	8	0	0	0	0	1	1	0	1	1	0	0	0	0	2	2
252	32	29	4	1	1	4 (-1)	2	2	2	1 (-1)	1 (-1)	3	2	2	3	2	2
333	14	14	0	2	2	0	1	1	0	1	1	0	2	2	0	1	1
398	14	13	0	2	2	0	2	2	0	1	1	0	1 (-1)	1	0	1	1
Total	139	134	7	11	11	9 (-1)	12	12	3 (-1)	8 (-1)	8 (-1)	5	10 (-1)	10	7	13	13

Supplementary Table 2: Acorn fates by landscape (urban/non-urban), year, canopy cover, and treatment. Summaries of fates across groups are included under "all."

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[1]	Year	Cover[2]	Treat[3]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
NU	2009	G	T	40	0	0.0	23	0.6	17	0.5	12	0.3	0	0.0	0	0.0	1	0.0	27	0.7	1	0.0	100.0	0	0.0	0.0
			P	40	0	0.0	28	0.8	12	0.3	5	0.1	0	0.0	16	0.4	18	0.5	1	0.0	7	0.2	38.9	2	0.1	28.6
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	80	0	0.0	51	1.4	29	0.8	17	0.5	0	0.0	16	0.4	19	0.5	28	0.8	8	0.2	42.1	2	0.1	25.0
		F	T	50	14	0.4	26	0.7	10	0.3	40	1.1	0	0.0	0	0.0	0	0.0	10	0.3	0	0.0	n/a	0	0.0	n/a
			P	50	19	0.5	29	0.8	2	0.1	27	0.7	0	0.0	12	0.3	11	0.3	0	0.0	8	0.2	72.7	6	0.2	75.0
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	100	33	0.9	55	1.5	12	0.3	67	1.8	0	0.0	12	0.3	11	0.3	10	0.3	8	0.2	72.7	6	0.2	75.0
		O	T	61	5	0.1	47	1.3	9	0.2	42	1.1	0	0.0	3	0.1	1	0.0	15	0.4	1	0.0	100.0	1	0.0	100.0
			P	59	2	0.1	49	1.3	8	0.2	22	0.6	0	0.0	12	0.3	23	0.6	2	0.1	12	0.3	52.2	10	0.3	83.3
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	120	7	0.2	96	2.6	17	0.5	64	1.7	0	0.0	15	0.4	24	0.6	17	0.5	13	0.3	54.2	11	0.3	84.6
		All	T	151	19	0.5	96	2.6	36	1.0	94	2.5	0	0.0	3	0.1	2	0.1	52	1.4	2	0.1	100.0	1	0.0	50.0
			P	149	21	0.6	106	2.8	22	0.6	54	1.4	0	0.0	40	1.1	52	1.4	3	0.1	27	0.7	51.9	18	0.5	66.7
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	300	40	1.1	202	5.4	58	1.6	148	4.0	0	0.0	43	1.2	54	1.4	55	1.5	29	0.8	53.7	19	0.5	65.5

[1] Landscape type: NU = non-urban; U = urban
[2] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[3] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[4]	Year	Cover[5]	Treat[6]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
NU	2010	G	T	50	9	0.2	0	0.0	41	1.1	10	0.3	0	0.0	0	0.0	0	0.0	40	1.1	0	0.0	n/a	n/a	n/a	n/a
			P	50	12	0.3	16	0.4	22	0.6	18	0.5	3	0.1	6	0.2	5	0.1	18	0.5	1	0.0	20.0	n/a	n/a	n/a
			S	50	11	0.3	0	0.0	39	1.0	21	0.6	0	0.0	5	0.1	0	0.0	24	0.6	0	0.0	n/a	n/a	n/a	n/a
			All	150	32	0.9	16	0.4	102	2.7	49	1.3	3	0.1	11	0.3	5	0.1	82	2.2	1	0.0	20.0	n/a	n/a	n/a
		F	T	90	53	1.4	4	0.1	33	0.9	74	2.0	0	0.0	0	0.0	0	0.0	16	0.4	0	0.0	n/a	n/a	n/a	n/a
			P	90	76	2.0	3	0.1	11	0.3	83	2.2	0	0.0	0	0.0	0	0.0	7	0.2	0	0.0	n/a	n/a	n/a	n/a
			S	90	76	2.0	3	0.1	11	0.3	87	2.3	1	0.0	0	0.0	0	0.0	2	0.1	0	0.0	n/a	n/a	n/a	n/a
			All	270	205	5.5	10	0.3	55	1.5	244	6.5	1	0.0	0	0.0	0	0.0	25	0.7	0	0.0	n/a	n/a	n/a	n/a
		O	T	100	48	1.3	5	0.1	47	1.3	58	1.6	0	0.0	0	0.0	0	0.0	42	1.1	0	0.0	n/a	n/a	n/a	n/a
			P	100	61	1.6	18	0.5	21	0.6	69	1.8	3	0.1	5	0.1	13	0.3	10	0.3	6	0.2	46.2	n/a	n/a	n/a
			S	100	71	1.9	2	0.1	27	0.7	80	2.1	0	0.0	7	0.2	5	0.1	8	0.2	4	0.1	80.0	n/a	n/a	n/a
			All	300	180	4.8	25	0.7	95	2.5	207	5.5	3	0.1	12	0.3	18	0.5	60	1.6	10	0.3	55.6	n/a	n/a	n/a
		All	T	240	110	2.9	9	0.2	121	3.2	142	3.8	0	0.0	0	0.0	0	0.0	98	2.6	0	0.0	n/a	n/a	0.0	n/a
			P	240	149	4.0	37	1.0	54	1.4	170	4.6	6	0.2	11	0.3	18	0.5	35	0.9	7	0.2	38.9	n/a	0.0	0.0
			S	240	158	4.2	5	0.1	77	2.1	188	5.0	1	0.0	12	0.3	5	0.1	34	0.9	4	0.1	80.0	n/a	0.0	0.0
			All	720	417	11.2	51	1.4	252	6.8	500	13.4	7	0.2	23	0.6	23	0.6	167	4.5	11	0.3	47.8	n/a	0.0	0.0

[4] Landscape type: NU = non-urban; U = urban
[5] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[6] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[7]	Year	Cover[8]	Treat[9]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
NU	2011	G	T	50	0	0.0	4	0.1	46	1.2	6	0.2	0	0.0	0	0.0	0	0.0	44	1.2	n/a	n/a	n/a	n/a	n/a	n/a
			P	50	1	0.0	6	0.2	43	1.2	18	0.5	3	0.1	0	0.0	5	0.1	24	0.6	n/a	n/a	n/a	n/a	n/a	n/a
			S	50	3	0.1	9	0.2	38	1.0	23	0.6	0	0.0	0	0.0	1	0.0	26	0.7	n/a	n/a	n/a	n/a	n/a	n/a
			All	150	4	0.1	19	0.5	127	3.4	47	1.3	3	0.1	0	0.0	6	0.2	94	2.5	n/a	n/a	n/a	n/a	n/a	n/a
		F	T	90	35	0.9	16	0.4	39	1.0	60	1.6	1	0.0	0	0.0	2	0.1	27	0.7	n/a	n/a	n/a	n/a	n/a	n/a
			P	90	42	1.1	7	0.2	41	1.1	70	1.9	2	0.1	0	0.0	5	0.1	13	0.3	n/a	n/a	n/a	n/a	n/a	n/a
			S	90	53	1.4	4	0.1	33	0.9	81	2.2	1	0.0	0	0.0	0	0.0	8	0.2	n/a	n/a	n/a	n/a	n/a	n/a
			All	270	130	3.5	27	0.7	113	3.0	211	5.7	4	0.1	0	0.0	7	0.2	48	1.3	n/a	n/a	n/a	n/a	n/a	n/a
		O	T	110	20	0.5	24	0.6	66	1.8	58	1.6	0	0.0	0	0.0	0	0.0	52	1.4	n/a	n/a	n/a	n/a	n/a	n/a
			P	110	33	0.9	30	0.8	47	1.3	75	2.0	1	0.0	0	0.0	11	0.3	23	0.6	n/a	n/a	n/a	n/a	n/a	n/a
			S	110	57	1.5	7	0.2	46	1.2	97	2.6	0	0.0	0	0.0	4	0.1	9	0.2	n/a	n/a	n/a	n/a	n/a	n/a
			All	330	110	2.9	61	1.6	159	4.3	230	6.2	1	0.0	0	0.0	15	0.4	84	2.3	n/a	n/a	n/a	n/a	n/a	n/a
		All	T	250	55	1.5	44	1.2	151	4.0	124	3.3	1	0.0	0	0.0	2	0.1	123	3.3	n/a	0.0	0.0	n/a	0.0	n/a
			P	250	76	2.0	43	1.2	131	3.5	163	4.4	6	0.2	0	0.0	21	0.6	60	1.6	n/a	0.0	0.0	n/a	0.0	n/a
			S	250	113	3.0	20	0.5	117	3.1	201	5.4	1	0.0	0	0.0	5	0.1	43	1.2	n/a	0.0	0.0	n/a	0.0	n/a
			All	750	244	6.5	107	2.9	399	10.7	488	13.1	8	0.2	0	0.0	28	0.8	226	6.1	n/a	0.0	0.0	n/a	0.0	n/a

[7] Landscape type: NU = non-urban; U = urban
[8] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[9] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[10]	Year	Cover[11]	Treat[12]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
NU	All	G	T	140	9	0.2	27	0.7	104	2.8	28	0.8	0	0.0	0	0.0	1	0.0	111	3.0	1	0.0	100.0	0	0.0	0.0
			P	140	13	0.3	50	1.3	77	2.1	41	1.1	6	0.2	22	0.6	28	0.8	43	1.2	8	0.2	28.6	2	0.1	25.0
			S	100	14	0.4	9	0.2	77	2.1	44	1.2	0	0.0	5	0.1	1	0.0	50	1.3	0	0.0	0.0	n/a	0.0	n/a
			All	380	36	1.0	86	2.3	258	6.9	113	3.0	6	0.2	27	0.7	30	0.8	204	5.5	9	0.2	30.0	2	0.1	22.2
		F	T	230	102	2.7	46	1.2	82	2.2	174	4.7	1	0.0	0	0.0	2	0.1	53	1.4	0	0.0	0.0	0	0.0	n/a
			P	230	137	3.7	39	1.0	54	1.4	180	4.8	2	0.1	12	0.3	16	0.4	20	0.5	8	0.2	50.0	6	0.2	75.0
			S	180	129	3.5	7	0.2	44	1.2	168	4.5	2	0.1	0	0.0	0	0.0	10	0.3	0	0.0	n/a	n/a	0.0	n/a
			All	640	368	9.9	92	2.5	180	4.8	522	14.0	5	0.1	12	0.3	18	0.5	83	2.2	8	0.2	44.4	6	0.2	75.0
		O	T	271	73	2.0	76	2.0	122	3.3	158	4.2	0	0.0	3	0.1	1	0.0	109	2.9	1	0.0	100.0	1	0.0	100.0
			P	269	96	2.6	97	2.6	76	2.0	166	4.5	4	0.1	17	0.5	47	1.3	35	0.9	18	0.5	38.3	10	0.3	55.6
			S	210	128	3.4	9	0.2	73	2.0	177	4.7	0	0.0	7	0.2	9	0.2	17	0.5	4	0.1	44.4	n/a	0.0	0.0
			All	750	297	8.0	182	4.9	271	7.3	501	13.4	4	0.1	27	0.7	57	1.5	161	4.3	23	0.6	40.4	11	0.3	47.8
		All	T	641	184	4.9	149	4.0	308	8.3	360	9.7	1	0.0	3	0.1	4	0.1	273	7.3	2	0.1	50.0	1	0.0	50.0
			P	639	246	6.6	186	5.0	207	5.5	387	10.4	12	0.3	51	1.4	91	2.4	98	2.6	34	0.9	37.4	18	0.5	52.9
			S	490	271	7.3	25	0.7	194	5.2	389	10.4	2	0.1	12	0.3	10	0.3	77	2.1	4	0.1	40.0	n/a	0.0	0.0
			All	1770	701	18.8	360	9.7	709	19.0	1136	30.5	15	0.4	66	1.8	105	2.8	448	12.0	40	1.1	38.1	19	0.5	47.5

[10] Landscape type: NU = non-urban; U = urban
[11] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[12] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[13]	Year	Cover[14]	Treat[15]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
U	2009	G	T	30	0	0.0	13	0.3	17	0.5	9	0.2	0	0.0	0	0.0	0	0.0	21	0.6	0	0.0	n/a	0	0.0	n/a
			P	30	1	0.0	25	0.7	4	0.1	4	0.1	12	0.3	0	0.0	13	0.3	1	0.0	13	0.3	100.0	10	0.3	76.9
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	60	1	0.0	38	1.0	21	0.6	13	0.3	12	0.3	0	0.0	13	0.3	22	0.6	13	0.3	100.0	10	0.3	76.9
		F	T	50	28	0.8	13	0.3	9	0.2	48	1.3	0	0.0	0	0.0	0	0.0	2	0.1	0	0.0	n/a	0	0.0	n/a
			P	50	10	0.3	27	0.7	13	0.3	20	0.5	0	0.0	24	0.6	6	0.2	0	0.0	1	0.0	16.7	1	0.0	100.0
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	100	38	1.0	40	1.1	22	0.6	68	1.8	0	0.0	24	0.6	6	0.2	2	0.1	1	0.0	16.7	1	0.0	100.0
		O	T	60	17	0.5	37	1.0	6	0.2	58	1.6	0	0.0	0	0.0	1	0.0	1	0.0	0	0.0	0.0	0	0.0	n/a
			P	60	4	0.1	52	1.4	4	0.1	39	1.0	1	0.0	4	0.1	16	0.4	0	0.0	13	0.3	81.3	10	0.3	76.9
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	120	21	0.6	89	2.4	10	0.3	97	2.6	1	0.0	4	0.1	17	0.5	1	0.0	13	0.3	76.5	10	0.3	76.9
		All	T	140	45	1.2	63	1.7	32	0.9	115	3.1	0	0.0	0	0.0	1	0.0	24	0.6	0	0.0	0.0	0	0.0	n/a
			P	140	15	0.4	104	2.8	21	0.6	63	1.7	13	0.3	28	0.8	35	0.9	1	0.0	27	0.7	77.1	21	0.6	77.8
			S	0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	n/a	n/a	0.0	n/a
			All	280	60	1.6	167	4.5	53	1.4	178	4.8	13	0.3	28	0.8	36	1.0	25	0.7	27	0.7	75.0	21	0.6	77.8

[13] Landscape type: NU = non-urban; U = urban
[14] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[15] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[16]	Year	Cover[17]	Treat[18]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
U	2010	G	T	60	7	0.2	4	0.1	49	1.3	14	0.4	0	0.0	0	0.0	0	0.0	46	1.2	0	0.0	n/a	n/a	n/a	n/a
			P	60	7	0.2	25	0.7	28	0.8	24	0.6	2	0.1	6	0.2	5	0.1	23	0.6	3	0.1	60.0	n/a	n/a	n/a
			S	60	12	0.3	8	0.2	40	1.1	24	0.6	0	0.0	2	0.1	1	0.0	33	0.9	0	0.0	0.0	n/a	n/a	n/a
			All	180	26	0.7	37	1.0	117	3.1	62	1.7	2	0.1	8	0.2	6	0.2	102	2.7	3	0.1	50.0	n/a	n/a	n/a
		F	T	100	96	2.6	0	0.0	4	0.1	97	2.6	0	0.0	0	0.0	0	0.0	3	0.1	0	0.0	n/a	n/a	n/a	n/a
			P	100	99	2.7	1	0.0	0	0.0	99	2.7	0	0.0	0	0.0	1	0.0	0	0.0	0	0.0	0.0	n/a	n/a	n/a
			S	100	98	2.6	0	0.0	2	0.1	99	2.7	0	0.0	0	0.0	0	0.0	1	0.0	0	0.0	n/a	n/a	n/a	n/a
			All	300	293	7.9	1	0.0	6	0.2	295	7.9	0	0.0	0	0.0	1	0.0	4	0.1	0	0.0	0.0	n/a	n/a	n/a
		O	T	120	87	2.3	12	0.3	21	0.6	94	2.5	1	0.0	0	0.0	0	0.0	25	0.7	0	0.0	n/a	n/a	n/a	n/a
			P	120	100	2.7	13	0.3	7	0.2	105	2.8	0	0.0	10	0.3	3	0.1	2	0.1	2	0.1	66.7	n/a	n/a	n/a
			S	120	105	2.8	7	0.2	8	0.2	108	2.9	0	0.0	9	0.2	2	0.1	1	0.0	1	0.0	50.0	n/a	n/a	n/a
			All	360	292	7.8	32	0.9	36	1.0	307	8.2	1	0.0	19	0.5	5	0.1	28	0.8	3	0.1	60.0	n/a	n/a	n/a
		All	T	280	190	5.1	16	0.4	74	2.0	205	5.5	1	0.0	0	0.0	0	0.0	74	2.0	0	0.0	n/a	n/a	0.0	n/a
			P	280	206	5.5	39	1.0	35	0.9	228	6.1	2	0.1	16	0.4	9	0.2	25	0.7	5	0.1	55.6	n/a	0.0	0.0
			S	280	215	5.8	15	0.4	50	1.3	231	6.2	0	0.0	11	0.3	3	0.1	35	0.9	1	0.0	33.3	n/a	0.0	0.0
			All	840	611	16.4	70	1.9	159	4.3	664	17.8	3	0.1	27	0.7	12	0.3	134	3.6	6	0.2	50.0	n/a	0.0	0.0

[16] Landscape type: NU = non-urban; U = urban
[17] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[18] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[19]	Year	Cover[20]	Treat[21]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
U	2011	G	T	60	2	0.1	12	0.3	46	1.2	12	0.3	0	0.0	0	0.0	0	0.0	48	1.3	n/a	n/a	n/a	n/a	n/a	n/a
			P	60	3	0.1	13	0.3	44	1.2	22	0.6	2	0.1	0	0.0	8	0.2	28	0.8	n/a	n/a	n/a	n/a	n/a	n/a
			S	60	3	0.1	8	0.2	49	1.3	17	0.5	0	0.0	0	0.0	1	0.0	42	1.1	n/a	n/a	n/a	n/a	n/a	n/a
			All	180	8	0.2	33	0.9	139	3.7	51	1.4	2	0.1	0	0.0	9	0.2	118	3.2	n/a	n/a	n/a	n/a	n/a	n/a
		F	T	100	71	1.9	2	0.1	27	0.7	88	2.4	0	0.0	0	0.0	2	0.1	10	0.3	n/a	n/a	n/a	n/a	n/a	n/a
			P	100	85	2.3	5	0.1	10	0.3	92	2.5	0	0.0	3	0.1	0	0.0	5	0.1	n/a	n/a	n/a	n/a	n/a	n/a
			S	100	96	2.6	1	0.0	3	0.1	97	2.6	0	0.0	2	0.1	1	0.0	0	0.0	n/a	n/a	n/a	n/a	n/a	n/a
			All	300	252	6.8	8	0.2	40	1.1	277	7.4	0	0.0	5	0.1	3	0.1	15	0.4	n/a	n/a	n/a	n/a	n/a	n/a
		O	T	120	54	1.4	21	0.6	45	1.2	74	2.0	2	0.1	0	0.0	0	0.0	44	1.2	n/a	n/a	n/a	n/a	n/a	n/a
			P	120	65	1.7	14	0.4	41	1.1	81	2.2	2	0.1	0	0.0	3	0.1	34	0.9	n/a	n/a	n/a	n/a	n/a	n/a
			S	120	71	1.9	15	0.4	34	0.9	84	2.3	4	0.1	0	0.0	2	0.1	30	0.8	n/a	n/a	n/a	n/a	n/a	n/a
			All	360	190	5.1	50	1.3	120	3.2	239	6.4	8	0.2	0	0.0	5	0.1	108	2.9	n/a	n/a	n/a	n/a	n/a	n/a
		All	T	280	127	3.4	35	0.9	118	3.2	174	4.7	2	0.1	0	0.0	2	0.1	102	2.7	n/a	0.0	0.0	n/a	0.0	n/a
			P	280	153	4.1	32	0.9	95	2.5	195	5.2	4	0.1	3	0.1	11	0.3	67	1.8	n/a	0.0	0.0	n/a	0.0	n/a
			S	280	170	4.6	24	0.6	86	2.3	198	5.3	4	0.1	2	0.1	4	0.1	72	1.9	n/a	0.0	0.0	n/a	0.0	n/a
			All	840	450	12.1	91	2.4	299	8.0	567	15.2	10	0.3	5	0.1	17	0.5	241	6.5	n/a	0.0	0.0	n/a	0.0	n/a

[19] Landscape type: NU = non-urban; U = urban
[20] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[21] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling			
Landscape[22]	Year	Cover[23]	Treat[24]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2	
U	All	G	T	150	9	0.2	29	0.8	112	3.0	35	0.9	0	0.0	0	0.0	0	0.0	115	3.1	0	0.0	n/a	0	0.0	n/a	
			P	150	11	0.3	63	1.7	76	2.0	50	1.3	16	0.4	6	0.2	26	0.7	52	1.4	16	0.4	61.5	10	0.3	62.5	
			S	120	15	0.4	16	0.4	89	2.4	41	1.1	0	0.0	2	0.1	2	0.1	75	2.0	0	0.0	0.0	n/a	0.0	n/a	
			All	420	35	0.9	108	2.9	277	7.4	126	3.4	16	0.4	8	0.2	28	0.8	242	6.5	16	0.4	57.1	10	0.3	62.5	
		F	T	250	195	5.2	15	0.4	40	1.1	233	6.2	0	0.0	0	0.0	2	0.1	15	0.4	0	0.0	0.0	0	0.0	n/a	
			P	250	194	5.2	33	0.9	23	0.6	211	5.7	0	0.0	27	0.7	7	0.2	5	0.1	1	0.0	14.3	1	0.0	100.0	
			S	200	194	5.2	1	0.0	5	0.1	196	5.3	0	0.0	2	0.1	1	0.0	1	0.0	0	0.0	0.0	n/a	0.0	n/a	
			All	700	583	15.6	49	1.3	68	1.8	640	17.2	0	0.0	29	0.8	10	0.3	21	0.6	1	0.0	10.0	1	0.0	100.0	
		O	T	300	158	4.2	70	1.9	72	1.9	226	6.1	3	0.1	0	0.0	1	0.0	70	1.9	0	0.0	0.0	0	0.0	n/a	
			P	300	169	4.5	79	2.1	52	1.4	225	6.0	3	0.1	14	0.4	22	0.6	36	1.0	15	0.4	68.2	10	0.3	66.7	
			S	240	176	4.7	22	0.6	42	1.1	192	5.1	4	0.1	9	0.2	4	0.1	31	0.8	1	0.0	25.0	n/a	0.0	0.0	
			All	840	503	13.5	171	4.6	166	4.5	643	17.2	10	0.3	23	0.6	27	0.7	137	3.7	16	0.4	59.3	10	0.3	62.5	
		All	T	700	362	9.7	114	3.1	224	6.0	494	13.2	3	0.1	0	0.0	3	0.1	200	5.4	0	0.0	0.0	0	0.0	n/a	
			P	700	374	10.0	175	4.7	151	4.0	486	13.0	19	0.5	47	1.3	55	1.5	93	2.5	32	0.9	58.2	21	0.6	65.6	
			S	560	385	10.3	39	1.0	136	3.6	429	11.5	4	0.1	13	0.3	7	0.2	107	2.9	1	0.0	14.3	n/a	0.0	0.0	
			All	1960	1121	30.1	328	8.8	511	13.7	1409	37.8	26	0.7	60	1.6	65	1.7	400	10.7	33	0.9	50.8	21	0.6	63.6	

[22] Landscape type: NU = non-urban; U = urban
[23] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[24] Acorn treatment: T = tagged; P = planted; S = surface

				Fall Fate							First Year Spring Fate											Second Year Spring Fate			Third Year Spring Fate	
				Handled		Germinated		Not Germinated			Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[25]	Year	Cover[26]	Treat[27]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
All	2009	G	T	70	0	0.0	36	1.0	34	0.9	21	0.6	0	0.0	0	0.0	1	0.0	48	1.3	1	0.0	100.0	0	0.0	0.0
			P	70	1	0.0	53	1.4	16	0.4	9	0.2	12	0.3	16	0.4	31	0.8	2	0.1	20	0.5	64.5	12	0.3	60.0
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	140	1	0.0	89	2.4	50	1.3	30	0.8	12	0.3	16	0.4	32	0.9	50	1.3	21	0.6	65.6	12	0.3	57.1
		F	T	100	42	1.1	39	1.0	19	0.5	88	2.4	0	0.0	0	0.0	0	0.0	12	0.3	0	0.0	n/a	0	0.0	n/a
			P	100	29	0.8	56	1.5	15	0.4	47	1.3	0	0.0	36	1.0	17	0.5	0	0.0	9	0.2	52.9	7	0.2	77.8
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	200	71	1.9	95	2.5	34	0.9	135	3.6	0	0.0	36	1.0	17	0.5	12	0.3	9	0.2	52.9	7	0.2	77.8
		O	T	121	22	0.6	84	2.3	15	0.4	100	2.7	0	0.0	3	0.1	2	0.1	16	0.4	1	0.0	50.0	1	0.0	100.0
			P	119	6	0.2	101	2.7	12	0.3	61	1.6	1	0.0	16	0.4	39	1.0	2	0.1	25	0.7	64.1	20	0.5	80.0
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	240	28	0.8	185	5.0	27	0.7	161	4.3	1	0.0	19	0.5	41	1.1	18	0.5	26	0.7	63.4	21	0.6	80.8
		All	T	291	64	1.7	159	4.3	68	1.8	209	5.6	0	0.0	3	0.1	3	0.1	76	2.0	2	0.1	66.7	1	0.0	50.0
			P	289	36	1.0	210	5.6	43	1.2	117	3.1	13	0.3	68	1.8	87	2.3	4	0.1	54	1.4	62.1	39	1.0	72.2
			S	0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	0.0	n/a	n/a	0.0	n/a
			All	580	100	2.7	369	9.9	111	3.0	326	8.7	13	0.3	71	1.9	90	2.4	80	2.1	56	1.5	62.2	40	1.1	71.4

[25] Landscape type: NU = non-urban; U = urban
[26] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[27] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[28]	Year	Cover[29]	Treat[30]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
All	2010	G		T	110	16	0.4	4	0.1	90	2.4	24	0.6	0	0.0	0	0.0	0	0.0	86	2.3	0	0.0	n/a	n/a	n/a
				P	110	19	0.5	41	1.1	50	1.3	42	1.1	5	0.1	12	0.3	10	0.3	41	1.1	4	0.1	40.0	n/a	n/a
				S	110	23	0.6	8	0.2	79	2.1	45	1.2	0	0.0	7	0.2	1	0.0	57	1.5	0	0.0	0.0	n/a	n/a
				All	330	58	1.6	53	1.4	219	5.9	111	3.0	5	0.1	19	0.5	11	0.3	184	4.9	4	0.1	36.4	n/a	n/a
		F		T	190	149	4.0	4	0.1	37	1.0	171	4.6	0	0.0	0	0.0	0	0.0	19	0.5	0	0.0	n/a	n/a	n/a
				P	190	175	4.7	4	0.1	11	0.3	182	4.9	0	0.0	0	0.0	1	0.0	7	0.2	0	0.0	0.0	n/a	n/a
				S	190	174	4.7	3	0.1	13	0.3	186	5.0	1	0.0	0	0.0	0	0.0	3	0.1	0	0.0	n/a	n/a	n/a
				All	570	498	13.4	11	0.3	61	1.6	539	14.5	1	0.0	0	0.0	1	0.0	29	0.8	0	0.0	0.0	n/a	n/a
		O		T	220	135	3.6	17	0.5	68	1.8	152	4.1	1	0.0	0	0.0	0	0.0	67	1.8	0	0.0	n/a	n/a	n/a
				P	220	161	4.3	31	0.8	28	0.8	174	4.7	3	0.1	15	0.4	16	0.4	12	0.3	8	0.2	50.0	n/a	n/a
				S	220	176	4.7	9	0.2	35	0.9	188	5.0	0	0.0	16	0.4	7	0.2	9	0.2	5	0.1	71.4	n/a	n/a
				All	660	472	12.7	57	1.5	131	3.5	514	13.8	4	0.1	31	0.8	23	0.6	88	2.4	13	0.3	56.5	n/a	n/a
		All		T	520	300	8.0	25	0.7	195	5.2	347	9.3	1	0.0	0	0.0	0	0.0	172	4.6	0	0.0	n/a	n/a	0.0	n/a
				P	520	355	9.5	76	2.0	89	2.4	398	10.7	8	0.2	27	0.7	27	0.7	60	1.6	12	0.3	44.4	n/a	0.0	0.0
				S	520	373	10.0	20	0.5	127	3.4	419	11.2	1	0.0	23	0.6	8	0.2	69	1.8	5	0.1	62.5	n/a	0.0	0.0
				All	1560	1028	27.6	121	3.2	411	11.0	1164	31.2	10	0.3	50	1.3	35	0.9	301	8.1	17	0.5	48.6	n/a	0.0	0.0

28 Landscape type: NU = non-urban; U = urban
29 Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
30 Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[31]	Year	Cover[32]	Treat[33]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
All	2011	G		T	110	2	0.1	16	0.4	92	2.5	18	0.5	0	0.0	0	0.0	0	0.0	92	2.5	n/a	n/a	n/a	n/a	n/a	n/a
				P	110	4	0.1	19	0.5	87	2.3	40	1.1	5	0.1	0	0.0	13	0.3	52	1.4	n/a	n/a	n/a	n/a	n/a	n/a
				S	110	6	0.2	17	0.5	87	2.3	40	1.1	0	0.0	0	0.0	2	0.1	68	1.8	n/a	n/a	n/a	n/a	n/a	n/a
				All	330	12	0.3	52	1.4	266	7.1	98	2.6	5	0.1	0	0.0	15	0.4	212	5.7	n/a	n/a	n/a	n/a	n/a	n/a
		F		T	190	106	2.8	18	0.5	66	1.8	148	4.0	1	0.0	0	0.0	4	0.1	37	1.0	n/a	n/a	n/a	n/a	n/a	n/a
				P	190	127	3.4	12	0.3	51	1.4	162	4.3	2	0.1	3	0.1	5	0.1	18	0.5	n/a	n/a	n/a	n/a	n/a	n/a
				S	190	149	4.0	5	0.1	36	1.0	178	4.8	1	0.0	2	0.1	1	0.0	8	0.2	n/a	n/a	n/a	n/a	n/a	n/a
				All	570	382	10.2	35	0.9	153	4.1	488	13.1	4	0.1	5	0.1	10	0.3	63	1.7	n/a	n/a	n/a	n/a	n/a	n/a
		O		T	230	74	2.0	45	1.2	111	3.0	132	3.5	2	0.1	0	0.0	0	0.0	96	2.6	n/a	n/a	n/a	n/a	n/a	n/a
				P	230	98	2.6	44	1.2	88	2.4	156	4.2	3	0.1	0	0.0	14	0.4	57	1.5	n/a	n/a	n/a	n/a	n/a	n/a
				S	230	128	3.4	22	0.6	80	2.1	181	4.9	4	0.1	0	0.0	6	0.2	39	1.0	n/a	n/a	n/a	n/a	n/a	n/a
				All	690	300	8.0	111	3.0	279	7.5	469	12.6	9	0.2	0	0.0	20	0.5	192	5.1	n/a	n/a	n/a	n/a	n/a	n/a
		All		T	530	182	4.9	79	2.1	269	7.2	298	8.0	3	0.1	0	0.0	4	0.1	225	6.0	n/a	0.0	0.0	n/a	0.0	n/a
				P	530	229	6.1	75	2.0	226	6.1	358	9.6	10	0.3	3	0.1	32	0.9	127	3.4	n/a	0.0	0.0	n/a	0.0	n/a
				S	530	283	7.6	44	1.2	203	5.4	399	10.7	5	0.1	2	0.1	9	0.2	115	3.1	n/a	0.0	0.0	n/a	0.0	n/a
				All	1590	694	18.6	198	5.3	698	18.7	1055	28.3	18	0.5	5	0.1	45	1.2	467	12.5	n/a	0.0	0.0	n/a	0.0	n/a

[31] Landscape type: NU = non-urban; U = urban
[32] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[33] Acorn treatment: T = tagged; P = planted; S = surface

					Fall Fate						First Year Spring Fate										Second Year Spring Fate			Third Year Spring Fate		
					Handled		Germinated		Not Germinated		Handled		Germinated		Not Germinated		Seedling		Dead		Seedling			Seedling		
Landscape[34]	Year	Cover[35]	Treat[36]	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	% all	% Year 1	n	% all	% Year 2
All	All	G	T	290	18	0.5	56	1.5	216	5.8	63	1.7	0	0.0	0	0.0	1	0.0	226	6.1	1	0.0	100.0	0	0.0	0.0
			P	290	24	0.6	113	3.0	153	4.1	91	2.4	22	0.6	28	0.8	54	1.4	95	2.5	24	0.6	44.4	12	0.3	50.0
			S	220	29	0.8	25	0.7	166	4.5	85	2.3	0	0.0	7	0.2	3	0.1	125	3.4	0	0.0	0.0	n/a	0.0	n/a
			All	800	71	1.9	194	5.2	535	14.3	239	6.4	22	0.6	35	0.9	58	1.6	446	12.0	25	0.7	43.1	12	0.3	48.0
		F	T	480	297	8.0	61	1.6	122	3.3	407	10.9	1	0.0	0	0.0	4	0.1	68	1.8	0	0.0	0.0	0	0.0	n/a
			P	480	331	8.9	72	1.9	77	2.1	391	10.5	2	0.1	39	1.0	23	0.6	25	0.7	9	0.2	39.1	7	0.2	77.8
			S	380	323	8.7	8	0.2	49	1.3	364	9.8	2	0.1	2	0.1	1	0.0	11	0.3	0	0.0	0.0	n/a	0.0	n/a
			All	1340	951	25.5	141	3.8	248	6.6	1162	31.2	5	0.1	41	1.1	28	0.8	104	2.8	9	0.2	32.1	7	0.2	77.8
		O	T	571	231	6.2	146	3.9	194	5.2	384	10.3	3	0.1	3	0.1	2	0.1	179	4.8	1	0.0	50.0	1	0.0	100.0
			P	569	265	7.1	176	4.7	128	3.4	391	10.5	7	0.2	31	0.8	69	1.8	71	1.9	33	0.9	47.8	20	0.5	60.6
			S	450	304	8.2	31	0.8	115	3.1	369	9.9	4	0.1	16	0.4	13	0.3	48	1.3	5	0.1	38.5	n/a	0.0	0.0
			All	1590	800	21.4	353	9.5	437	11.7	1144	30.7	14	0.4	50	1.3	84	2.3	298	8.0	39	1.0	46.4	21	0.6	53.8
		All	T	1341	546	14.6	263	7.1	532	14.3	854	22.9	4	0.1	3	0.1	7	0.2	473	12.7	2	0.1	28.6	1	0.0	50.0
			P	1339	620	16.6	361	9.7	358	9.6	873	23.4	31	0.8	98	2.6	146	3.9	191	5.1	66	1.8	45.2	39	1.0	59.1
			S	1050	656	17.6	64	1.7	330	8.8	818	21.9	6	0.2	25	0.7	17	0.5	184	4.9	5	0.1	29.4	n/a	0.0	0.0
			All	3730	1822	48.8	688	18.4	1220	32.7	2545	68.2	41	1.1	126	3.4	170	4.6	848	22.7	73	2.0	42.9	40	1.1	54.8

[34] Landscape type: NU = non-urban; U = urban
[35] Canopy cover type: G = non-forested grassland; F = conifer forest; O = oak
[36] Acorn treatment: T = tagged; P = planted; S = surface