# Parcel-scale development and landscaping actions affect vegetation, bird, and fungal communities on office developments

Karen L. Dyson

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Reading Committee:

Gordon Bradley, Chair

Ken Yocom

Jon Bakker

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## Abstract

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Karen L. Dyson

Chair of the Supervisory Committee:
Professor Emeritus Gordon Bradley
Environmental and Forest Sciences

Habitat loss and degradation are primary drivers of extinction and reduced ecosystem function in urban social-ecological systems. While creating local reserves and restoring degraded habitat are important, they are incomplete responses. The matrix, including the built environment, in which these preserves are located must also provide resources for local species. Urban ecosystems can be used to achieve conservation goals by altering human actions to support local species' habitat needs. I ask what outcomes of development, landscaping, and maintenance actions taken at the parcel scale explained variation in vegetation, bird, and fungal community composition on office developments in Redmond and Bellevue, Washington, USA. These include measures of tree preservation,

planting choices, and resource inputs. I compared these with neighborhood and site scale socio-economic variables and neighborhood scale land cover variables found significant in previous urban ecology studies (Heezik et al., 2013; Lerman and Warren, 2011; Loss et al., 2009; Munyenyembe et al.,1989).

I found that variables describing the outcome of development and landscaping actions were associated with tree community composition and explained variation in shrub, winter passerine, and fungal community composition. Other variables, including those found significant in previous research, were not significant. Additionally, I observed a wide variety of vegetation communities on office developments, suggesting significant habitat variation within one land use type. My results provide insight into two pieces of social-ecological urban ecosystems. First, the outcomes of human development and landscaping action are related to differences in vegetation communities, and second, that these differences in vegetation community composition—and particularly tree community structure—are related to differences in winter passerine and fungal community composition. My results suggest that there is the potential to alter human actions in the built environment matrix to support local species, including native bird and fungal taxa in the Puget Trough. Important next steps include cultivating landscapes with native trees and revising land use code. The variation in vegetation I observed also suggests that future urban ecology research design must account for within and between land use variability.

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To my husband, friends, and family—you're the best. Thank you for being with me <3

# Dedication

To my father—I will love you always.

# Chapter 1

# Introduction

> "Conservation is paved with good intentions which prove to be futile, or even dangerous, because they are devoid of critical understanding either of the land, or of economic land-use." (p 225; Leopold, 1989)

Habitat loss, degradation, and fragmentation are primary drivers of local extinction and reduced ecosystem function in urban socio-ecological systems and other anthropogenic habitat (Alberti, 2005; Alberti et al., 2003; Polasky et al., 2005; Rosenzweig, 2003). Creating local reserves and restoring degraded habitat are important but incomplete responses to habitat loss. Isolated reserves possess insufficient area to adequately preserve species diversity (Rosenzweig, 2003).

If conservation efforts are to be successful in urbanizing regions, the matrix in which preserves are situated, including the built environment, must provide sufficient resources for local species and maintain ecosystem integrity (Fahrig, 2001; Fischer et al., 2006; Miller and Hobbs, 2002; Polasky et al., 2005; Rosenzweig, 2003). In the United States, this will require working with private landowners to alter private actions in support of conservation (Goddard et al., 2010; Miller and Hobbs, 2002).

Our understanding of how to manipulate the built environment to support conservation is in its early stages (Chapman et al., 2017). Scientific research investigating the relationship between human action, ecosystem processes, and patterns of community diversity and composition in urban ecosystems is needed to inform policy and guide landowner actions. To this end, my research examines how human actions contributing to ecosystem processes may impact the patterns of organisms in cities, and which actions may better reconcile human land use and conservation goals.

Two heuristics provide useful context. First, social-ecological system theory, which emphasizes that human and natural systems are irreparably intertwined in urbanizing ecosystems and provides a framework for incorporating traditional ecosystem concepts into urban ecosystems, and second, reconciliation ecology, which advocates for practicing conservation in urbanizing ecosystems.

## 1.1 Social-ecological systems

Social-ecological systems (SES) theory conceptualizes urban ecosystems and other anthropogenic ecosystems as complex systems where elements of the social and ecological spheres are fundamentally connected. Cities are emergent phenomena of socio-economic and biophysical forces (Alberti et al., 2003; Liu et al., 2007; Redman et al., 2004). Events occurring in one part of the system will affect many other parts of the system, and feedback loops and thresholds may arise from the non-linear relationships between different parts of the system (Alberti et al., 2003; Liu et al., 2007). Social-ecological systems are also heterogeneous across time, space, and organizational units (Liu et al., 2007; Redman et al., 2004).

Ecologists' view of the relationship between society and nature has historically varied between co-dependence and opposition (Hill, 2005). For example, restoration ecology frequently frames human actions *within* an ecosystem e.g. grassland management as drivers *external to* the ecosystem (Lavorel et al., 2013). Social-ecological systems theory considers humans part of the ecosystem and human actions as an integral process in these ecosystems. That is, humans act within the ecosystem as one of a suite of species, and anthropogenic disturbance processes are natural disturbance processes (Alberti et al., 2003; Grimm et al., 2000; Hill, 2005; Redman et al., 2004), though the scale of human action when compared with other organisms requires special consideration (Nassauer, 1997). Ecosystem processes in urban ecosystems include erosion, migration, predation, community development, moving earth/nutrients/species, and disturbances (Alberti et al., 2003; Nassauer, 1997). These processes operate at multiple interrelated scales, from global (e.g. climate change; Sukopp and Wurzel, 2003) to small scales (e.g. homeowner plant choice; Faeth et al., 2011). This framework highlights the agency of people who own or manage land on shaping woody vegetation communities, impacting birds, fungal communities, and the broader urban ecosystem.

Social-ecological systems frameworks like those developed by Alberti (2005), Grimm et al. (2000), Collins et al. (2011), and others can help frame questions about interactions between different human actors (e.g. does land use policy alter landowner behavior?), between different components of the ecosystem (e.g. questions of predation) and between our species and the species with which we share space (e.g. questions of ecosystem services provision and press/pulse disturbance events). They also allow us to examine different combinations of human agents and the scales at which they influence land use and ecosystem process (Alberti, 2008, 2005; Collins et al., 2011; Grimm et al., 2000; Pickett et al., 1997; Redman et al., 2004).

## 1.2 Ecosystem processes in social-ecological systems

In socio-ecological systems, human actions contribute significantly to disturbance and succession processes, which in turn are key drivers of spatial landscape patterns (Turner, 2005). Some frameworks explicitly incorporate these traditional ecosystem concepts into social-ecological systems (Alberti, 2008; Collins et al., 2011).

**Development as disturbance:** Disturbance refers to "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White, 1985; Turner, 2005). In urban ecosystems, agents of disturbance may be physical, biotic, or social; that is, both human action (e.g. development) and natural events (e.g. hurricane) contribute to disturbance processes. However as humans are themselves part of social-ecological systems, not every human action should be considered a disturbance (Grimm et al., 2017).

Disturbance can be disaggregated into three key phenomena: drivers, mechanisms, and impact (Peters et al., 2011). Drivers are endogenous or exogenous, and provide either a pulse or press of influence on the system. In the Puget Trough area, human disturbances like development have replaced climate-related physical events like fire as the primary endogenous disturbance driver; this will likely continue based on projected population increases of approximately 10,000 people/year in King County (Dorney et al., 1984; Gibb and Hochuli, 2002; Halpern and Spies, 1995; Peters et al., 2011; Washington State Office of Financial Management, 2017). Development is an important example of a pulse disturbance, while press disturbances include increasing foot traffic and vegetation disturbance at parks due to higher populations.

The mechanisms of disturbance for development, particularly the dominant ‘tabula rasa’ style of development, include removing vegetation and topsoil and compacting soil with heavy equipment (Grimm et al., 2017). Impacts of development include changes in patch structure and configuration, legacy vegetation, soil communities, altering plant establishment, seed bank reduction or removal, altered soil hydrology, and impaired soil-air gas exchange, mycorrhizal growth, and root growth (Alberti, 2005; Franklin, 1997; Gibb and Hochuli, 2002; Hope et al., 2003; Pickett et al., 2001).

Development as disturbance also interacts with other natural disturbance events. For example, in the Puget Trough, the pattern of tall conifer trees remaining after site development disturbance—usually narrow rows or small clusters of trees—are more susceptible to windthrow. Human action can also change the magnitude, frequency, and intensity of natural disturbances, such as floods or erosion (Alberti, 2008; Peters et al., 2011).

Where development of a site is the primary disturbance there, many other discrete human activities contribute to secondary disturbance processes. For example, pruning shrubs and mowing grass and application of herbicides and pesticides converts materials from one pool (live plants) to another (dead vegetation moved off site; Grimm et al., 2017). However, this level of disaggregation is not useful here; I use an aggregated view of disturbance because I am more interested in the outcomes of primary development disturbance (e.g. the effect of legacy vegetation) and ongoing secondary processes including succession and ongoing site management.

**Vegetation succession processes:** Multiple processes determine the path of vegetation succession following disturbance, including dispersal, establishment, competition, and mortality. In social ecological systems, vegetation succession is influenced by natural succession processes, including wind dispersal and regeneration from seed banks, and socially mediated vegetation management by humans (Grimm et al., 2017).

Most of new plant material in urban areas is chosen and planted by people (Faeth et al., 2011). Landscape design and planting has largely replaced succession processes in urban ecosystems including dispersal and plant establishment. For example, landscaping choices facilitate long-distance dispersal by removing climactic limitations on plants and requirements for natural propagule dispersal (Niinemets and Peñuelas, 2008). Vegetation management also alters competition processes. Where humans have planted vegetation, native species that could colonize urbanizing landscapes may be precluded from doing so by competition (Shochat et al., 2006), and thus competition with established exotics may reduce biodiversity (Marzluff et al., 2001). Plant productivity and mortality is altered by fertilizer, irrigation, and other inputs (Faeth et al., 2011; LeBauer and Treseder, 2008; Lepczyk et al., 2004).

## 1.3 Reconciliation ecology

Reconciliation ecologists suggest that social-ecological systems can and should be used to avoid species extinctions and conserve biodiversity by manipulating the built environment to support conservation (Lundholm and Richardson, 2010). In cities, reconciliation ecology focuses on the urban matrix to support species which tolerate human presence and protect species and biodiversity in adjacent reserves. For example, recent research found that surrounding vegetation composition supports urban natural remnants, which supports using reconciliation ecology as a conservation tool in urban ecosystems (Fernández et al., 2018). Reconciliation ecology also promotes using the unique conditions found in urban ecosystems to promote conservation. For example, urbanizing areas with limited resources may provide ideal areas for species adapted to nutrient or water poor environments as they will not face competition from other species (Rebele, 1994).

Reconciliation ecology is largely based on the theory of island biogeography and the inadequacy of remnant and restored habitat area to conserve biodiversity due to species-area relationships (i.e. the number of species generally increases with increasing area; Lundholm and Richardson, 2010; Zimmerman and Bierregaard, 1986). The theory of island biogeography postulates that biodiversity at the patch and regional scales is an equilibrium governed by the compensatory processes of colonization and the extinction of species. Although originally developed by Robert MacArthur and E.O. Wilson to describe biodiversity on islands, island biogeography has been expanded to include any system where habitat patches (islands) are surrounded by a matrix of other habitats (ocean). At equilibrium, these colonization rates—and evolution plays a part too, on much longer time scales—are balanced by extinction rates, which island biogeography suggests is governed by habitat area. Larger islands or patches have the potential to support more individuals of a species, reducing the risk of extinction from stochastic environmental events (disturbance, genetic drift, etc.).

Based on this traditional model of island biogeography, reconciliation ecology attempts to conserve biodiversity by altering the parameters of the species-area relationship and the equilibrium theory of island biogeography. For species that can tolerate the presence of humans, reconciliation ecology suggests designing the built environment itself to create larger areas of habitat to support larger populations of more species. These larger habitat islands should then help reduce extinctions as larger populations are less susceptible to extinction from stochasticity (Rosenzweig, 2003, 2001). For species that cannot tolerate human presence, reconciliation ecology can act as a buffer around habitat remnants, effectively increasing "core" habitat area. For mobile species, designing the built environment to increase the permeability of the urban matrix (i.e. facilitate movement) reduces the effective distance between habitat islands and increases local populations' persistence and the probability of colonization (Niemelä, 1999; Ricketts, 2001). At a species level, the potential conservation benefits of this approach are limited by species behavior—for example, species that require large ranges (large carnivores) require that large parcels of land be set aside for their use.

However, by focusing on island biogeography, reconciliation ecology presents a simplified model of population dynamics. The habitat amount and habitat quality (continuum) hypotheses add constructively to models of species richness and abundance (Gardiner et al., 2018). The habitat amount hypothesis suggests that habitat amount in an area should replace patch/island size and isolation, as both variables are driven by the effect of sample area (Fahrig, 2013). This hypothesis has been supported by some studies, though in others patch size and isolation were better predictors (Gardiner et al., 2018; Hanski, 2015; Melo et al., 2017; Torrenta and Villard, 2017). The habitat quality hypothesis suggests that species occupancy occurs as a gradient within a landscape driven by ecological processes (Gardiner et al., 2018; Hanski, 2015). Habitat quality is relative and will vary for each species based on habitat requirements, adaptability, and the specific ways in which habitat is degraded in the urban matrix (Mortelliti et al., 2010). These additional theories do not negate reconciliation ecology, and may provide additional avenues for conservation.

Therefore, we must increase habitat quality in addition to habitat area in the urban matrix to preserve biodiversity in urbanizing ecosystems. Habitat area provides an upper bound on the number of organisms that can hypothetically live in an area, but habitat quality may determine what proportion of this potential is realized (Hanski, 2015; Rosenzweig, 2003). For reconciliation ecology to be successful, it must focus not only on breadth (how many acres) but also on depth (which habitat types and their quality). Understanding and successfully designing land parcels in accordance to local species' habitat needs then becomes the central concern, both for parcels that are 'island' habitat for a species or managed to increase the permeability of the matrix (Ricketts, 2001; Rosenzweig, 2003, 2001; Zimmerman and Bierregaard, 1986). Research studies focusing on population dynamics of individual species and communities in urban areas and iterative ecological design will be critical to our success. While reconciliation ecology researchers are aware of this, there is a tendency in the literature to not publish poor outcomes (Francis and Lorimer, 2011).

In keeping with the reconciliation ecology framework, this dissertation is written from an explicit normative standpoint that developers and landscape architects need to consider the larger implications of development on ecosystem function and biodiversity at multiple scales. Developers and landscape architects also need to avoid 'formulaic' responses that homogenize the broader urban matrix, a phenomenon observed in the commodification of wetland restoration.

## 1.4 Research questions

To support biodiversity conservation in urban ecosystems, my research asks: "*What outcomes of human actions in urban ecosystems explain variation in community composition present on office developments?*" I examine how the outcomes of site-scale human actions contributing to urban ecosystem processes—specifically actions taken during development and when landscaping and maintaining sites—impact patterns of vegetation, bird, and fungal communities. For these groups I asked:

1. What tree and shrub communities exist on office developments? What variables describing socio-economic conditions and/or variables describing the outcome of development, landscap-

ing, or maintenance actions explain variation in tree and shrub community structure?

2. What bird species exhibit associations with native or cultivated vegetation communities in office developments? What variables describing neighborhood-scale socio-economic or land cover patterns and/or variables describing the outcome of development, landscaping, or maintenance actions explain variation in bird or foraging bird effective species richness or community composition?
3. What variables describing neighborhood-scale socio-economic or land cover patterns and/or variables describing the outcome of development, landscaping, or maintenance actions explain variation in effective species richness, community composition, or trophic-specific community composition of fungal taxa? Is there evidence of community thresholds (simultaneous changes in multiple taxa abundance) in fungal communities along ecosystem gradients for significant variables?

I use the term “land management” to incorporate all stages of landscaping design, installation, and maintenance of plantings and ground cover on a developed parcel; I use “landscaping” to refer specifically to design and installation of vegetation plantings, and “maintenance” to actions contributing to site upkeep. Collectively, land management includes landscape architecture, planting activities, and maintenance activities, all of which contribute to ecosystem processes within the social-ecological system. I compare these site-scale actions with neighborhood and site-scale socio-economic variables and neighborhood-scale land cover variables found significant in other urban ecology studies (Heezik et al., 2013; Lerman and Warren, 2011; Loss et al., 2009; Munyenyembe et al., 1989).

My research goal is to articulate how human actions contributing to ecosystem processes may impact the patterns of organisms in cities, and which actions may better reconcile human land use and conservation goals. Though important, my work does not address mechanisms influencing community structure, nor does it examine motivations behind the actions taken by landowners and developers.

I chose to study woody vegetation, winter passerine birds, and fungi on office developments for multiple reasons. Each of these taxa represents an important aspect of the ecosystems present

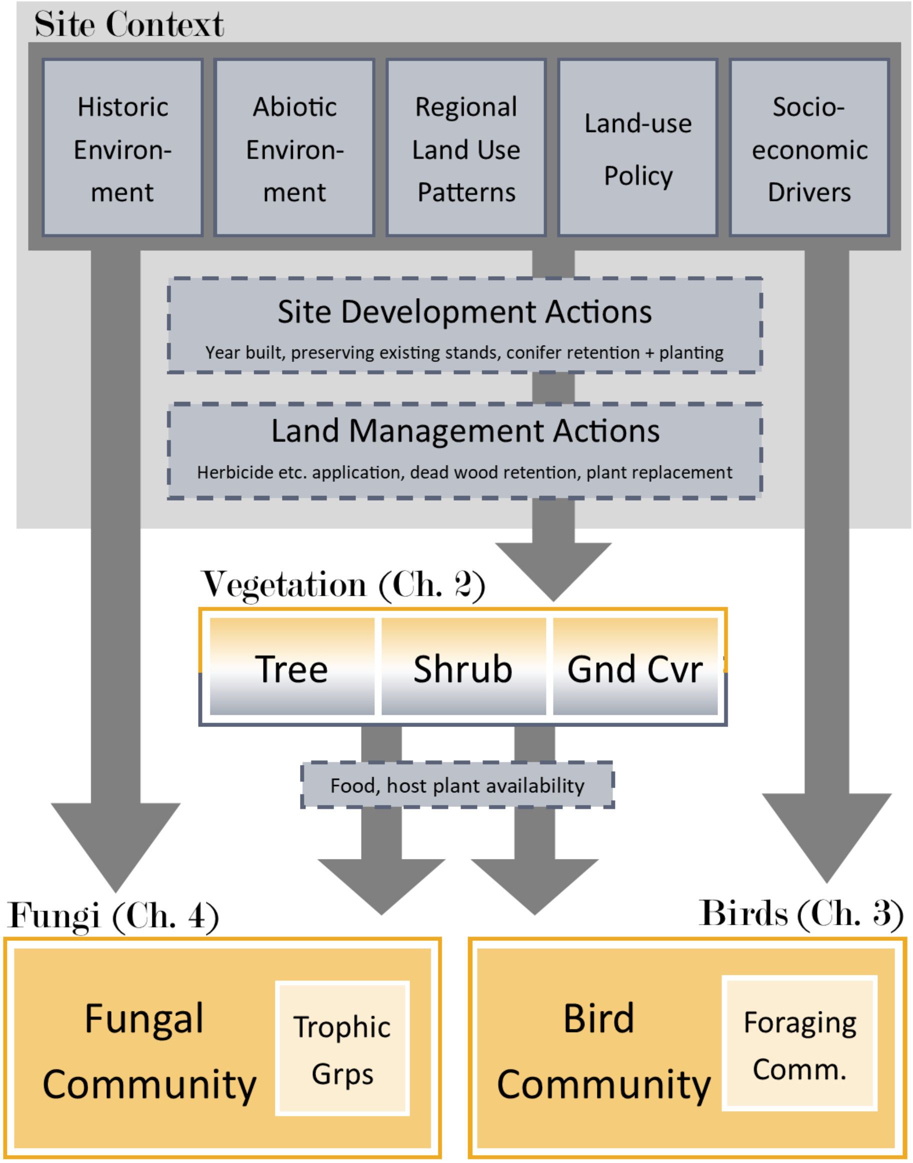

Figure 1.1: A conceptual diagram describing variable relationships considered in this study. Ecosystem patterns are drawn with solid outlines, while ecosystem processes have dashed outlines. Independent variables are gray, while dependent variables are orange. Vegetation and ground cover variables fulfill both roles. Site context includes variables from both social and ecological spheres in both current and previous time steps. Site development actions and land management actions function as pulse disturbance sensu Collins et al. (2011). I hypothesize in Chapter 2 that the outcome of site development and land management actions explains variation in tree and shrub community composition and ground cover present on site. In Chapters 3 and 4, I hypothesize that these vegetation and ground cover variables, along with site context variables, explain variation in bird and fungal communities.

on office developments and provides important ecosystem services to human communities (Figure 1.1). Woody vegetation (trees and shrubs) provides most of the habitat available to higher trophic levels, including birds and fungi (Faeth et al., 2011). In the Pacific Northwest, large native conifers like Douglas-fir provide important microhabitat for native bird species, and are an indicator for biodiversity (Michel and Winter, 2009). Woody vegetation is also responsible for aesthetic components of the landscape important to humans and community identity, as well as key ecosystem services like shade provision, rainwater interception, carbon sequestration, and primary production (Collins et al., 2011; Elmendorf, 2008; Wolf, 2005). As a result, many municipalities in the Puget Sound region and beyond have adopted tree protection policies, canopy cover goals, and vegetation planting policies (Young, 2011).

Passerine bird species feed directly on woody vegetation (flowers, buds, berries) and also on the insects that this vegetation supports (Poole, 2016). In the winter, bird species' dietary preferences are more inclusive, and urban vegetation could provide birds with critical food resources for winter survival and breeding success in the following year (Faaborg et al., 2010; Poole, 2016). Birds are highly mobile species, and are sensitive to variation in vegetation structure, and patterns of bird habitat use may therefore provide information on the resources available at an office development (Croci et al., 2008). Birds, including those associated with forest habitat, have been used as indicators of biodiversity globally (e.g. Butchart et al., 2010) and in urban ecosystems (e.g. Blair, 1999). Birds provide ecosystem services, including eating pests, dispersing seeds, pollinating flowers, and otherwise modifying the environment in ecologically important ways (Whelan et al., 2015). Birds are also charismatic, and provide cultural ecosystem services important to large numbers of citizens (Collins et al., 2011; Whelan et al., 2015). Humans' positive views of birds is linked to landowner willingness to alter landscapes in ways that are beneficial to birds and potentially other species (White et al., 2018).

The fungal community is also closely tied to the vegetation community. Fungi decompose dead vegetation and have parasitic and mycorrhizal relationships with living vegetation. Fungal communities are sensitive to changes in vegetation communities, nutrient availability, global change, and soil chemistry (Lilleskov et al., 2002; Lothamer et al., 2014; Newbound et al., 2012). Changes in fungal community structure may in turn impact woody vegetation growth and resilience to global change, and mycorrhizal fungi regulate development, biodiversity, and productivity of ecosystems (Peay et al., 2010; Suz et al., 2015). Fungi contribute to urban ecosystem function and vegetation health as important components of ecosystem processes including decomposition and nutrient provision to mutualistic vegetation (Lilleskov et al., 2002; Lothamer et al., 2014). Fungi are also cultural resources, with many cultures valuing them for food and medicine. As a result, researchers have proposed monitoring fungi to improve forest management, including for urban forests (Suz et al., 2015).

Overall, the three taxonomic groups provide varied and important information about the urban ecosystem. Where woody vegetation is largely controlled by humans, bird and fungal distributions are not (Faeth et al., 2011). Vegetation provides critical habitat for birds and fungi, while birds and fungi occupy very different places in the urban food web. Birds are mobile and exhibit complex habitat use patterns, while fungi are immobile and dependent on the resources present at a site in order to thrive (Müller et al., 2013; Peay et al., 2010). Birds are well studied in urban systems, while fungi are poorly studied (Newbound et al., 2010). The two taxonomic groups have very different life history requirements, ecological niches, and provide different ecosystem services to humans; together, birds and fungi serve as proxies for biodiversity.

I chose to study office developments as a land use frequented by many urban residents, providing opportunities for environmental education, but infrequently included in urban ecology research (Blair, 1999; Snep, 2009). I define office developments as planned developments with one or more office buildings designed to conduct commercial business, set in landscaped grounds with shared amenities including parking lots. This definition includes business parks, office parks, and medical/dental offices.

Finally, I focus on the Cities of Redmond and Bellevue in the State of Washington in the United States of America to reduce environmental variability between study sites. Office developments in Redmond and Bellevue are relatively large parcels of private property (50% are over 1.2 acres, with the largest 42.5 acres), and have a history of heterogeneous land management practices (Chapter 2). These properties are managed either by the property owner or a hired property manager; property owners or managers may oversee one property or multiple, with some firms controlling significant numbers of properties in the region (e.g. CBRE, Davis). Therefore, influencing property owners or managers to change their actions to support conservation may have a broad impact in terms of acres.

This dissertation is organized into five chapters. In Chapter 2 I describe tree and shrub communities on office developments, and identify variables which explain variation in community structure. I found that vegetation communities are highly variable across office developments, and that development and landscaping actions best explain this variability. Studies using a limited number of sites per land use are potentially drawing incorrect conclusions about vegetation and habitat potential (McIntyre et al., 2000). In Chapter 3 I quantify the bird and foraging bird community observed on site and find that both bird effective species richness and bird communities are significantly influenced by development and landscaping actions influencing the vegetation community. In Chapter 4 I quantify the fungal community using next-generation sequencing techniques and mushroom collections and find that fungal effective species richness and community composition and trophic guild community composition are significantly influenced by development and landscaping actions taken by developers and landowners. Chapter 5 provides an overview of my research and urban ecology broadly for practicing planners, landscape architects, and others, and discusses practical steps for modifying development and landscaping actions to support urban ecosystems (Luederitz et al., 2015). Finally, Chapter 6 concludes by examining what my research contributes to the literature and important future research directions.

# Chapter 2

# Woody vegetation communities on office developments are heterogenous

## 2.1 Introduction

Humans in social-ecological systems exert a strong influence on vegetation community composition and functional diversity, which in turn influences habitat quantity and quality and ecosystem service provision (Byrne, 2007; Faeth et al., 2011; Lehmann et al., 2014). Understanding how human actions influence vegetation communities and resulting habitat quality and quantity available to other trophic levels in the urban matrix facilitates decisionmaking to support local species via reconciliation ecology.

Human actions when developing, landscaping, and maintaining urban land contribute to processes that determine patterns of vegetation community composition and distribution in socio-ecological systems (Avolio et al., 2018; Faeth et al., 2011; Lehmann et al., 2014). In western Washington, development has replaced fire as the primary disturbance driver and precursor to new forest stands [Gibb and Hochuli (2002); Walcott (1899); Sharpe et al. (1986); County Assessor (n.d.); Notes (1864); (Halpern and Spies, 1995). Development and fire as drivers of disturbance differ in significant ways, including the relative size of disturbed patches, the length of disturbance, and the matrix surrounding the disturbed area (Gibb and Hochuli, 2002; Marzluff, 2008; Pickett et al., 2008). In general, historic fires in western Washington were large and on a long (200-400 year) time scale, though medium and low intensity fires also occurred (Stine et al., 2014). Fire was an ecological management tool used in the region by Coast Salish tribes to maintain food and other material production (Boyd, 1999; Charnley et al., 2008).

The mechanisms of disturbance for development, particularly the dominant “tabula rasa” style of development, include removing vegetation and topsoil and compacting soil with heavy equipment (Grimm et al., 2017; Turner, 2005). Vegetation patterns impacted include community composition, distribution, patch structure, legacy vegetation, plant establishment, and seed banks (Alberti, 2005; Gibb and Hochuli, 2002; Mullaney et al., 2015; Peters et al., 2011; Pickett et al., 2001). Choices made at the time of development influence future site conditions; for example, preserving existing trees determines legacy vegetation and important stand characteristics like tree age (Figure 2.1; Dorney et al., 1984).

Multiple processes determine the path of vegetation succession following disturbance. In social-ecological systems, both natural succession processes, including wind dispersal and regeneration from seed banks, and socially mediated vegetation management influence vegetation succession (Grimm et al., 2017). However, landscape design and planting have largely replaced dispersal and plant establishment processes contributing to succession (Dorney et al., 1984; Faeth et al., 2011; Goodness, 2018; Heezik et al., 2014; Widrlechner, 1990). On private property, landowner decisions drive species selection and community composition. Plantings are generally ornamental introduced shrubs, trees, or mowed grasses, though recently the use of native species in landscaping has become more common (Blair, 1996; Burghardt et al., 2009; Faeth et al., 2011; Germaine et al., 1998; Heezik et al., 2014; McKinney, 2002). These choices are informed by a complex mix of trends in landscape design, office development marketing, regulations, landscape budget, expert opinion, and plant availability (Avolio et al., 2018; Conway, 2016; Widrlechner, 1990). On residential properties, neighborhood socio-economic variables including neighborhood age and wealth may explain much of the variation in planting choices (Avolio et al., 2018; Clarke et al., 2013; Hope et al., 2003; Leong et al., 2018).

Once planted, developed parcels require significant energy and material inputs to maintain the

Figure 2.1: Time series of a commercial development project located in Redmond, WA showing typical tabula rasa style development where all vegetation and topsoil is removed or altered. a. Clearing the site of vegetation. b. Grading the site and digging foundation. Photos taken by the author four weeks apart in 2015.

desired aesthetic. As a result, vegetation succession in urban areas is more static than it would be otherwise (Zipperer, 2010). Weeding and herbicide application are activities that arrest succession and maintain the landscape in the desired state by altering plant life history traits via human-induced plant death (Faeth et al., 2011). Competition and natural selection are altered by adding fertilizers and water to urban vegetation, often in favor of planted ornamental species (Faeth et al., 2011; LeBauer and Treseder, 2008; Lepczyk et al., 2004; Zipperer, 2010).

Woody vegetation is also responsible for aesthetic components of the landscape important to humans and community identity, as well as key ecosystem services like shade provision, rainwater interception, carbon sequestration, and primary productivity (Collins et al., 2011; Elmendorf, 2008; Wolf, 2005). As a result many municipalities in the Puget Sound region and beyond have adopted tree protection policies, canopy cover goals, and vegetation planting policies (Young, 2011).

These local land use policies directly influence development and landscaping actions (Conway, 2016; Goodness, 2018). Four types of local land use policies are particularly important in the Pacific Northwest. First, clearing and grading activities that occur during development, including removing vegetation and excavating and grading soils, require permits (Agnelli et al., 2004; Andres and Smith, 2004; Byrne, 2007; Dorney et al., 1984; Faeth et al., 2011; Halpern and Spies, 1995; McKinney, 2002; Pickett et al., 2009). Second, maximum impervious surface cover is often specified, along with minimum parking space requirements. Together these effectively sets a minimum allowable impervious surface cover (DeLaria, 2008; Environmental Protection Agency, 2011). Third, tree preservation policies impact office development inventory of large trees and influence provision of native tree habitat. Finally, following construction, developers are required to plant landscaping around the new building. Screening unsightly views and creating breaks between land uses—not habitat provision—are commonly cited motivations for landscape design requirements. Along with trees retained through tree preservation policies, these landscape plantings represent a significant portion of the vegetation on site and of the habitat quality and quantity available to other organisms (Avolio et al., 2018; Faeth et al., 2011).

Overall, the combination of planted, spontaneous, and remnant natives and introduced species create unique vegetation communities and patterns (McKinney, 2002; Wittig, 2010). Since local biological communities are largely determined by available vegetation, landowner choices in planting vegetation impact food webs and biodiversity (Avolio et al., 2018; Faeth et al., 2011). For example, the proportion of native insect species is correlated with the proportion of native plant species, and introduced ornamentals are unlikely to support the same insect species, or the same biomass or diversity of fauna that existed previously at the site (Burghardt et al., 2009; Crisp et al., 1998; McKinney, 2002; Rebele, 1994). If insect populations and biomass change due to cultivated ornamental vegetation, it follows that species at higher trophic levels would also be impacted (Burghardt et al., 2009; Faeth et al., 2011; Marzluff et al., 2001). In the Pacific Northwest, large native conifers like Douglas-fir provide important microhabitat for native bird species and their insect prey (Michel and Winter, 2009).

Though frequently overlooked, the vegetation habitat available to organisms in the urban matrix can contribute to local biodiversity conservation. Habitat loss, degradation, and fragmentation are primary drivers of extinction and declines in ecosystem function, particularly in urban ecological systems and other anthropogenic habitat (Alberti, 2005; Alberti et al., 2003; Polasky et al., 2005; Rosenzweig, 2003). Isolated reserves possess insufficient area to adequately preserve species diversity (Rosenzweig, 2003). For conservation efforts to be successful in urbanizing regions, the matrix in which preserves are situated, including the built environment, must provide sufficient resources for local species (Fahrig, 2001; Fischer et al., 2006; Miller and Hobbs, 2002; Polasky et al., 2005; Rosenzweig, 2003). This will require working with private landowners to alter private actions to support conservation of locally important vegetated habitat (Goddard et al., 2010; Miller and Hobbs, 2002).

In this chapter I examine the link between socio-economic patterns, human actions, and observed patterns of vegetation on office developments (Figure 2.2). I address two key questions:

1. What tree and shrub communities exist on office developments as a result of current and historical human actions?
2. What variables describing socio-economic conditions or variables describing the outcome of development, landscaping, or maintenance actions explain variation in tree and shrub community structure?

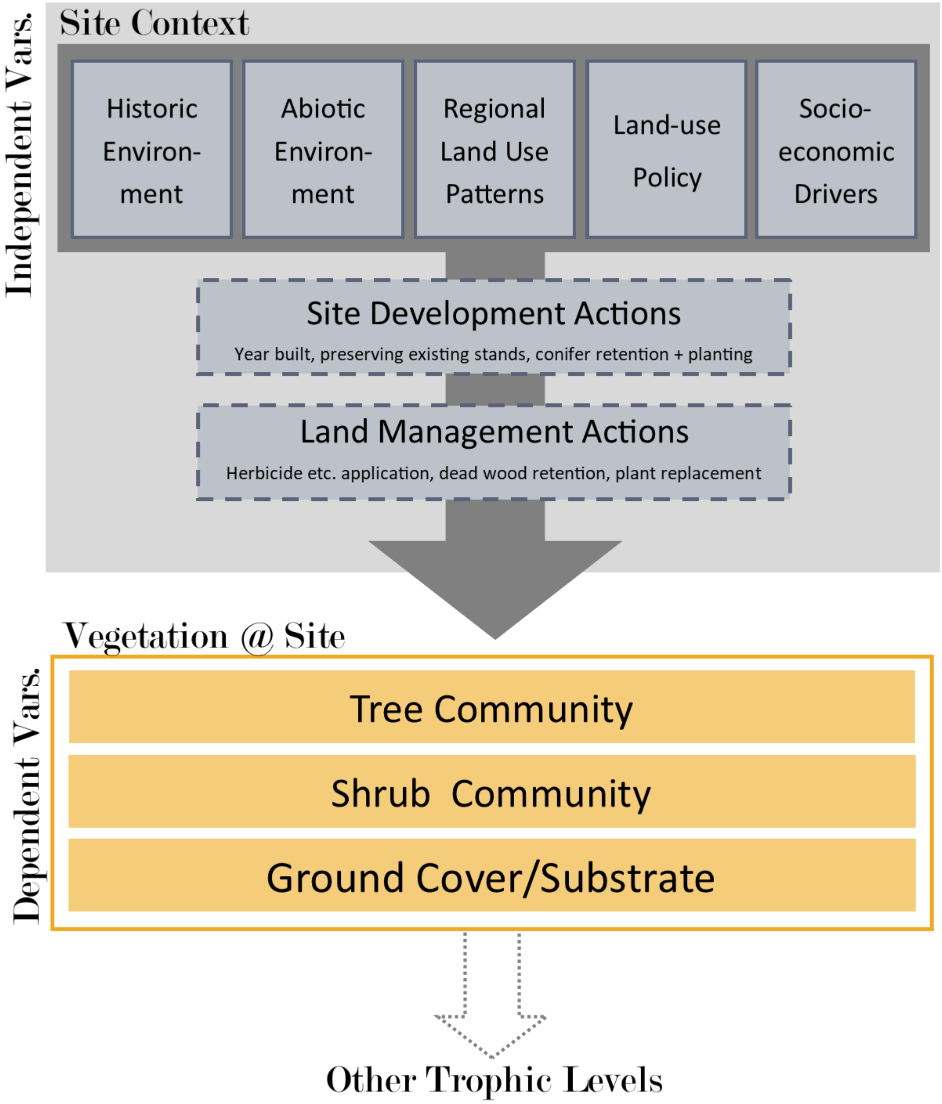

Figure 2.2: An overview of the relationships between site context and human action variables and the vegetation community present at a site. When a site is developed, the developer's actions determine whether stands of trees are preserved through development, and the initial conifer density (both preserved and planted), the initial planting design (both ornamental trees and shrubs), and the year built. These variables are further modified by subsequent land management actions, which include herbicide/pesticide/etc. applications, dead wood removal, and plant replacement (replacing dead plants or refreshing the planting design). The resulting vegetation on the site (tree and shrub communities and ground cover) influence ecosystem services provided, including habitat available to other trophic levels.

While vegetation surveys in urban areas have classified vegetation communities and examined human actions on residential neighborhoods and public open space (Dana et al., 2002; Hope et al., 2003; Lehmann et al., 2014), this research has generally not been extended to other land use types including office developments and other commercial land uses (Bourne and Conway, 2014a; Snep et al., 2011). This oversight means that there are important land uses in cities for which we lack information about the composition of vegetation communities. Land uses are complex socio-economic constructs where a diversity of agents and decision makers—often different for each land use—interact with a rapidly evolving urban ecosystem.

I hypothesize that vegetation communities on office developments are heterogeneous. Based on what previous vegetation research in social-ecological systems, I hypothesize that neighborhood socio-economic variables found significant in explaining vegetation patterns on residential property will not be significant on office developments (commercial property), and that site-scale socio-economic variables will be significant in explaining vegetation patterns, including site age and property value.

I quantified the tree and shrub communities and ground cover area on office developments in Redmond and Bellevue, Washington, USA. I gathered information on the outcomes of development, landscaping, and management actions and used public databases to quantify socio-economic variables. As I focused on examining outcomes to assess and guide policy, I did not address developer or landowner choice or motivation, only the results of their actions and management decisions. I used cluster analysis to identify tree and shrub community types, and multivariate ecology tools including PERMANOVA and NMDS to identify variables explaining tree and shrub community structure.

I found that vegetation communities are highly variable across office developments, and that development and landscaping actions best explain this variability. Additionally, studies using a limited number of sites per land use are potentially drawing incorrect conclusions about vegetation and habitat potential (McIntyre et al., 2000). Unlike residential property, variation in vegetation communities on office developments are explained more by development and land management actions and are not driven by socio-economics. This suggests a need for land use policy to be informed by ecological findings, and that altering human action may impact habitat quality and quantity available for other organisms.

## 2.2 Materials and Methods

### 2.2.1 Study area

Redmond (2017 population 64,000) and Bellevue (population 144,000) are located east of Seattle in King County, Washington (United States Census Bureau, 2017). Both cities share a similar ecological history, a similar disturbance timeline for logging and agriculture, and have grown considerably since the opening of the Evergreen Point Floating Bridge (SR 520) in 1963. They are at similar elevations ($< 500$ ft) and experience the same climate and weather. The sampling frame was limited to Redmond and Bellevue north of I-90 and excluded developments in Bellevue's central business district.

### 2.2.2 Site selection

I used disproportionate stratified random sampling to ensure that my sample included sites across the entire vegetation gradient. Approximately 600 office development parcels met the initial study criteria defined by assigned land use from King County Assessor's Office. I grouped adjacent parcels into units of analysis to ensure that my units of analysis were based on site management. Adjacent parcels with the same owner and with buildings built within three years of one another were grouped. All parcels not meeting these criteria were left as individual parcels. This resulted in 491 potential study sites (Figure 2.3).

I classified the vegetation at each potential study site into rough categories using a brief visual estimation during site visits in early 2014 (Figure 2.4). High vegetation sites were approximately 1/3 covered by larger native conifer cover and more than 5 native shrub genus richness (genus visible on brief inspection; 10 sites); medium canopy sites had the conifer cover requirement without the native shrub richness requirement (22 sites); medium diverse sites had the native shrub richness requirement without the canopy cover requirement (53 sites); medium vegetation sites were

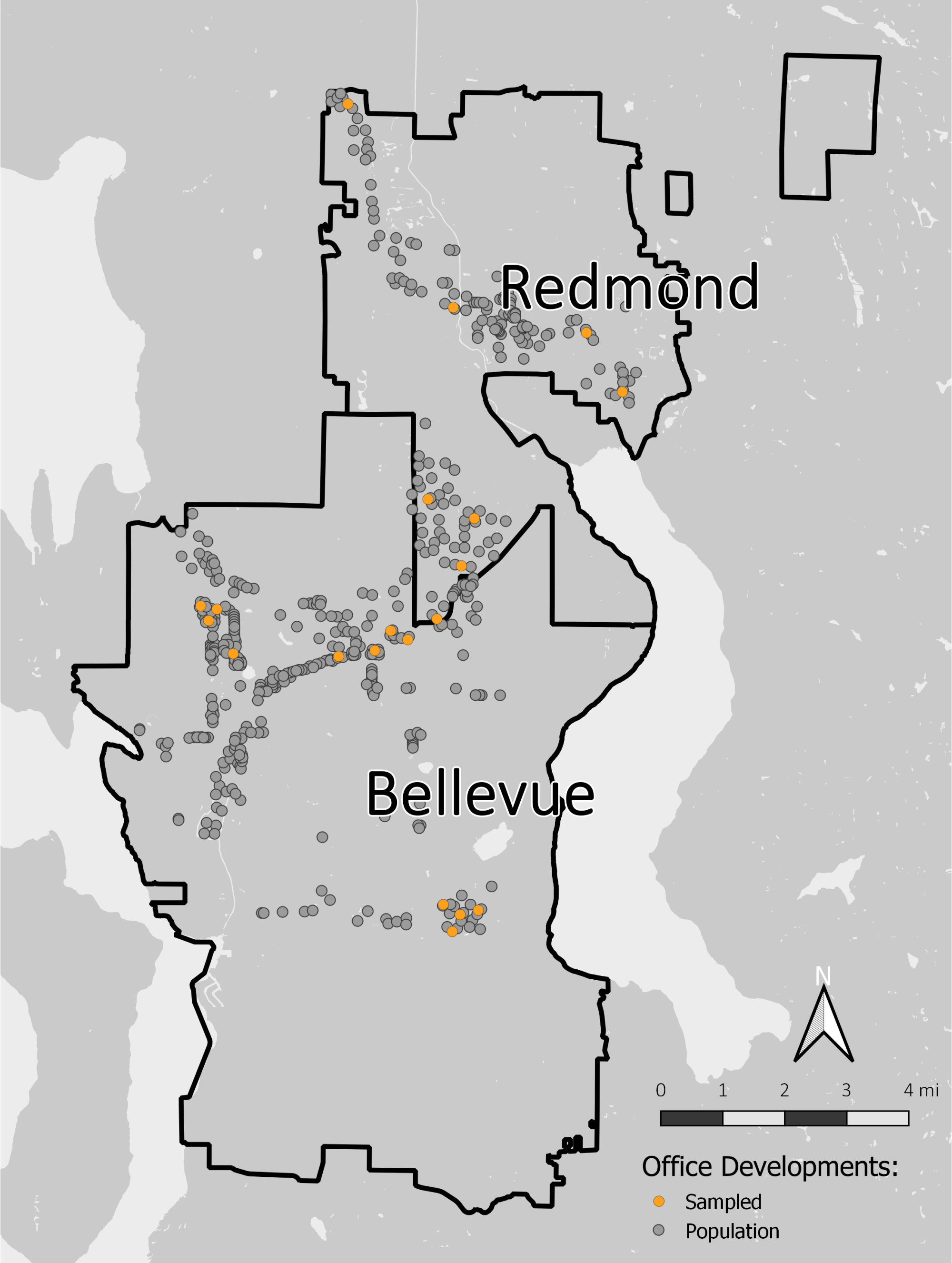

Figure 2.3: Map of office development study sites in Redmond and Bellevue, Washington. The population of office developments is represented with gray circles, while sampled sites are shown with orange circles.

approximately 1/6 covered by any canopy cover with 5+ total shrub genus richness (264 sites; and low vegetation sites had less than 1/10 canopy cover and fewer than 5 total shrub genus richness (56 sites). Sites with no vegetation, with wetlands, or those that were currently under construction or undergoing landscape replanting were excluded from the analysis (87 sites). The remaining pool of potential sites had no notable hydrological features like wetlands or streams on site, were located away from large waterbodies, and most had a similar, minimal slope.

I used these 5 vegetation categories to conduct stratified random sampling (405 potential sites). To avoid confounding factors, I restricted the sampling pool to sites in the 25th to 85th percentile for area and the 15th to 85th percentile for surrounding impervious surfaces. I requested property access through three mailings sent to the property owner or manager on file in the King County Assessor's database (Dyson et al., 2018). In the second and third rounds of mailings, I targeted sites belonging to vegetation categories that were underrepresented in the sample to ensure that I sampled across the entire vegetation gradient.

My final sample of 20 sites included 5 high, 3 medium canopy, 4 medium diverse, 3 medium, and 5 low vegetation sites. Of 46 mailed requests, 20 (43.5%) received no response or were not deliverable. Of the 26 (56.5%) responses received, 6 (23.1%) of were rejected, and 20 (76.9%) were accepted. Sampled sites ranged from 0.631 acres to 5.39 acres in size. 13 sites were located in Bellevue and 7 sites were located in Redmond. The office developments on study sites were built between 1975 and 2008. Commercial use of the sites included light industrial, white collar office space, and medical/dental offices. Some sites were fully leased to tenants, while others were either partly or fully owner-occupied. Company size ranged from less than 10 to many thousand employees.

### 2.2.3 Vegetation data collection

I censused vegetation communities in summer of 2015. Each tree and shrub was identified to species or genus (Dirr, 2009, 1997; Sibley and others, 2009). Trees with DBH $<$ 4" were considered saplings and not included in analysis due to time limitations. This size was chosen to include all potential "significant" trees in Redmond and Bellevue's zoning codes, which are greater than 6" or 8" DBH. Following Daniels and Kirkpatrick (2006a), conifers under 2 m were grouped into a broad class

Figure 2.4: Examples of each vegetation category, from top left to bottom right: High (HH); Medium Canopy (MC); Medium Diverse (MD); Medium (MM); Low (LL); no vegetation (LP; excluded); wetlands (WW; excluded).

of dwarf conifer species. Unidentified individuals of both were given a unique identifier code for multivariate community analysis. Some tree species were grouped at the genus level due to the abundance of very similar cultivars in the landscaping trade, including *Prunus* sp. and *Malus* sp.

Tree and shrub genera were assigned to one of three provenance categories—native, non-native, or ambiguous—based on range information from the United States Geological Survey and the United States Department of Agriculture (U.S. Geological Survey, 1999; USDA, 2016). The ambiguous category was used for genera including both native and non-native cultivated species that are difficult to distinguish, and/or frequently interbred and sold as crosses. For example, some *Mahonia* sp. were native (tall Oregon grape *M. aquifolium* and low Oregon grape *M. nervosa*), while others originate in Asia (Leatherleaf mahonia, *Mahonia japonica*) and many hybrids are bred and sold by nurseries (e.g. *Mahonia x media* “Charity”).

### 2.2.4 Ground cover data collection

Broad ground cover material types were recorded on paper maps, then hand digitized in QGIS to calculate area (QGIS Development Team, 2016). Note that ground cover is used here to include any material at ground level rather than the narrower usage referring just to herbaceous plants. Pervious cover types recorded include dense vegetation, dirt/litter, grass (turf grass including moss and forb species), gravel, dense ivy, mulch, and water. Individual turf, moss, and forb species were not recorded due to the diversity present in urban areas and time limitations.

### 2.2.5 Independent variable calculation

Independent variables used in this analysis are defined in Table 2.1. Data on the socio-economic properties of sampled sites at both parcel- and neighborhood-scale were obtained from multiple public sources (Homer et al., 2015; King County Department of Assessments, 2014; King County GIS Center, 2014; United States Census Bureau, 2016; Xian et al., 2011). While assessed land value is included, assessed building value could not be included due to a high number of irregularities in the dataset. Missing assessed land values were replaced with the median land value for the entire population.

Neighborhood socio-economic variables were chosen based on previous studies on residential and public property and calculated in QGIS (Dana et al., 2002; Grove et al., 2014; Hope et al., 2003; Martin et al., 2004; Walker et al., 2009). Decisions on commercial properties are likely driven by different motivations and preferences; however I included these variables to determine if patterns found in residential property are also applicable to commercial property and if characteristics of the surrounding residential property impacted office developments. These include median income and percent of the population born outside of the United States. For commercial specific variables, I included building quality, as assigned by the King County Assessor's Office as a proxy for the grades assigned to commercial property on market which affect property value. I also included size, building age, and a measure of the land rent gradient (appraised value/area). I attempted to use other variables (e.g. appraised value per built sqft, previous land use) however the available data was either incorrect or incomplete. For example, some buildings received tax breaks following the 2008 recession, so their appraised value was listed as $1,000 when the building's market value was significantly more ($5,000,000+).

I calculated three variables describing development and landscaping actions from site observations of the tree community. First, the height of five dominant native conifers (in practice, Douglas-fir or western red cedar) at each site were measured using a Nikon Forestry Pro Laser Rangefinder. Median tree height served as a proxy for tree age, as tree cores were not collected due to liability concerns (Dyson et al., 2018). Second, I used a combination of historical records and site construction plans to determine whether each site had a stand of 3 adjacent tree predating site development. These stands of trees are second growth regeneration following the widespread logging that occurred between 1890-1910 (County Assessor, n.d.; Walcott, 1899). Third, I summed the number of individual Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) observed to calculate native conifer count.

I derived variables describing maintenance actions from interviews with site landscaping services and property owners. I conducted interviews based on a master set of questions following the expert interview technique (Dexter, 1970; Harvey, 2011). The master set of questions can be found in Appendix A: Vegetation. In total, 17 interviews were completed, with two interviewees managing two sites each. Thirteen interviews were with landscaping professionals, including the two with multiple sites, and four were with the property owner. I supplemented these interviews with observational data from site visits over the course of two years (11-15 visits per site). I obtained site maintenance information for 19 sites in this way; for one site I was unable to contact the landscaper and relied on observation. I assigned a value (Yes, No, or Unknown) to maintenance variables based on interview data. After tallying responses, I removed "Insecticide" and "Fungicide" application variables from further consideration as there were no "Yes" responses.

I also censused dead wood (logs, snags and stumps) at each site. Logs were defined as fallen dead wood more than 6" in diameter; snags were standing dead wood more than 6" diameter and more than 6' tall; and stumps were standing dead wood not meeting this height requirement, not including shrub stumps. Multi-trunk stumps were counted only once. Stumps where the tree had grown from a co-dominant trunk were included.

### 2.2.6 Data transformations

I standardized tree and shrub abundance data by total site area (acres) to allow for consistent comparison between sites. This transformation preserves parcel boundaries as the unit of analysis and reflects developer and landowner actions during and following development that determine the amount of plantible area, the number of trees preserved, and the number of trees and shrubs planted. Between site standardization (e.g. as is used in Wisconsin standardization) was not used as the vegetation on all sites was completely censused. Ground cover data was also standardized by the total area of the study site.

### 2.2.7 Data Analysis

Woody vegetation analysis methods are summarized in Figure 2.5.

#### Identifying vegetation community typologies

I used flexible beta clustering and indicator species analysis to determine vegetation community typologies on office developments. I used the agnes {vegan} function with beta = -0.5 to reduce

Table 2.1: Definition of independent variables used in woody vegetation analysis.

| **Variable Name** | Definition | Data Source |
|---|---|---|
| **1.** | **SOCIO-ECONOMIC SITE AND NEIGHBORHOOD** | |
| **Area (acre)** | Site area, in acres. | King County Assessor |
| **Town** | Location, Bellevue or Redmond. | King County Assessor |
| **Building Age (in 2017)** | Age of building on site (or mean age for multiple buildings) in 2017. | King County Assessor |
| **Building Quality** | Categorical 'quality class' assigned to buildings on the site | King County Assessor |
| **Appraised Land Value per Acre** | Appraised land value divided by site area. One missing assessed land values were replaced with population median land value. | King County Assessor |
| **Impervious w/in 500 m (%)** | Percent impervious surface within 500 m of the site's perimeter. | National Land Cover Database 2011 Percent Developed Imperviousness dataset updated in 2014 |
| **Median Income** | The median income of residents for the site's block group | American Community Survey 2014 5-year block group |
| **Percent Foreign-Born** | The percent of residents born outside of the United States for the site's block group. | American Community Survey 2014 5-year block group |
| **2.** | **DEVELOPMENT, LANDSCAPE, AND MAINTENANCE** | |
| **Stands Predate Development** | Binary variable indicating presence of a cluster of three+ trees that predate development. (Development) | Site survey |
| **Median Height of Dominant Douglas-fir** | Median height (m) of five dominant Douglas-fir; age proxy. (Development) | Site survey |
| **Density of Native Conifers** | Total density of Douglas-fir, western redcedar, and western hemlock (Development/Landscaping). | Site survey |
| **Cleanup** | Binary variable indicating whether the landscaping crew removes detritus from the site. (Maintenance) | Interviews and site survey |
| **Irrigation** | Binary variable indicating whether irrigation is used during the summer months. (Maintenance) | Interviews and site survey |
| **Mulch, Herbicide, and/or Fertilizer Application** | Binary variables (3) indicating whether landscaping crew applies mulch, herbicides, or fertilizers to a site. (Maintenance) | Interviews and site survey |
| **Dead Wood (count)** | Total abundance of stumps, logs, and snags on site. (Maintenance) | Site survey |

Table 2.2: Summary statistics for independent variables for both the population of office developments in Redmond and Bellevue and the sample of sites studied (87 and 20 sites, respectively). Sites were selected based on area and percent impervious. Median income ($) and % foreign born are included to compare patterns in commercial developments with patterns found significant in residential research.

| Metric | Minimum | Maximum | Mean | S.D. | Median |
|---|---|---|---|---|---|
| Sample: Area (acres) | 0.63 | 5.39 | 2.57 | 1.58 | 2.45 |
| Population: Area (acres) | 0.03 | 42.51 | 3.21 | 5.17 | 1.20 |
| Sample: Percent Impervious w/in 500m | 48.75 | 66.96 | 56.76 | 6.29 | 55.66 |
| Population: Percent Impervious w/in 500m | 19.33 | 81.11 | 56.31 | 12.07 | 57.78 |
| Sample: Year Built | 1975 | 2008 | 1984.92 | 9.77 | 1982.00 |
| Population: Year Built | 1911 | 2013 | 1981.85 | 14.09 | 1983.00 |
| Sample: Median Income ($) | 42368 | 134643 | 80477.50 | 22179.18 | 73754.00 |
| Population: Median Income ($) | 38804 | 194107 | 81808.41 | 24175.64 | 80750.00 |
| Sample: Percent Foreign-Born | 0.15 | 0.86 | 0.41 | 0.18 | 0.37 |
| Population: Percent Foreign-Born | 0.15 | 0.86 | 0.39 | 0.16 | 0.40 |

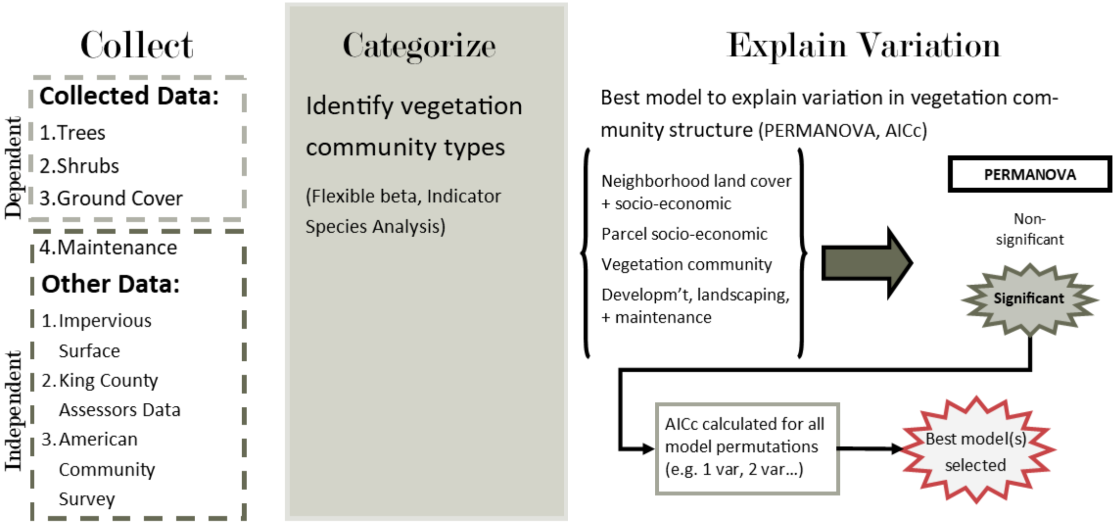

Figure 2.5: Summary of vegetation data analysis methods.

chaining and produce an ecologically interpretable dendrogram (Breckenridge, 2000; Dufrêne and Legendre, 1997; McCune et al., 2002; Milligan, 1989; Oksanen et al., 2017).

Indicator species analysis, which assesses the predictive values of species as indicators of the conditions at site groups, was performed using multipatt {indicspecies} (De Caceres and Legendre, 2009; De Cáceres, 2013a; De Cáceres et al., 2010). I ran the permutation-based function 100 times, kept only indicator species present in $> 50\%$ of the runs, and took the mean of the indicator statistics generated for each species.

### Explaining variation in tree and shrub community structure

**PERMANOVA:** PERMANOVA is a permutation based implementation of ANOVA/MANOVA that avoids assumptions about underlying distributions of community structure and can be used with non-Euclidian distance matrices (Anderson, 2001). I used the adonis2 {vegan} PERMANOVA implementation (Oksanen et al., 2017). I used a multi-step approach to avoid transforming independent variables or using ordination to collapse related variables, as these actions make results less interpretable for urban planners and other professionals without back transformation. I first tested each variable individually in PERMANOVA (simple multivariate regression). I used ANOVA to test for significant differences in dispersion for categorical variables (anova(betadisper()) {stats} {vegan}, Oksanen et al., 2017). I then constructed models using all variables with significant pseudo-$F$ values ($\alpha \leq 0.05$) in all possible single and multiple variable model combinations. I used a custom AICc function based on Residual Sums of Squares to compare models and identify those with the best support.

**NMDS:** Non-metric multidimensional scaling (NMDS) is a rank-based ordination technique that is robust to data without identifiable distributions, can be used with any distance or dissimilarity measure (McCune et al., 2002). I used 100 repetitions of the metaMDS {vegan} implementation of NMDS to find a stable minima (McCune et al., 2002; Oksanen et al., 2017).

**Mantel tests:** Mantel tests were used to test for correlation between ground cover and tree and shrub community composition. I used the mantel {vegan} function with Bray-Curtis distance to calculate the test statistic (Oksanen et al., 2017).

Table 2.3: Summary statistics for tree and shrub communities on sampled sites.

| Metric | Minimum | Maximum | Mean | S.D. | Median |
|---|---|---|---|---|---|
| Site Area (acres) | 0.63 | 5.39 | 2.57 | 1.58 | 2.45 |
| Tree Effective Species Richness (exp(H')) | 1.90 | 8.75 | 4.76 | 1.89 | 4.71 |
| Tree Abundance | 10.00 | 240.00 | 98.90 | 64.40 | 86.00 |
| Native Conifer Abundance All Sizes | 0.00 | 216.00 | 49.80 | 57.58 | 28.00 |
| Native Conifer Density All Sizes (#/acre) | 0.00 | 61.29 | 22.47 | 19.25 | 19.73 |
| Shrub Effective Species Richness (exp(H')) | 5.68 | 21.14 | 10.74 | 3.59 | 10.38 |
| Shrub Abundance | 71.00 | 1789.00 | 401.95 | 439.02 | 220.50 |
| Shrub Density (#/acre) | 39.65 | 404.01 | 153.06 | 99.70 | 125.66 |
| Native Shrub Species Richness | 0.00 | 10.00 | 4.00 | 2.62 | 4.00 |

Table 2.4: Summary statistics for ground cover on sampled sites.

| Metric | Minimum | Maximum | Mean | Median |
|---|---|---|---|---|
| Percent Impervious | 43.04 | 81.52 | 66.44 | 70.97 |
| Percent Pervious | 18.48 | 56.96 | 33.56 | 29.04 |
| .....Percent Dense Vegetation | 0.00 | 20.50 | 3.05 | 0.44 |
| .....Percent Dirt & Litter | 0.00 | 26.96 | 5.96 | 1.21 |
| .....Percent Grass | 0.00 | 19.10 | 7.28 | 6.53 |
| .....Percent Ivy | 0.00 | 20.95 | 5.30 | 3.09 |
| .....Percent Mulch | 0.26 | 28.04 | 11.81 | 10.91 |
| .....Percent Other | 0.00 | 1.26 | 0.16 | 0.00 |

## 2.3 Results and Discussion

I observed 52 taxa of trees (11 native, 1978 individuals) and 85 taxa of shrubs (16 native, 8039 individuals). There are differences in tree and shrub abundance, density, and effective species richness across the 20 office developments sampled (Table 2.3; Appendix A: Vegetation). The proportion of impervious surface and relative abundance of previous ground covers also varied (Table 2.4). I did not observe a relationship between site area and percent pervious surface area (Pr(>|t|) = 0.924).

### 2.3.1 Identifying vegetation community typologies

Cluster analysis identified two tree community typologies and two shrub community typologies, which I named "Native" and "Ornamental" community typologies (flexible beta = -0.5; agglomer-

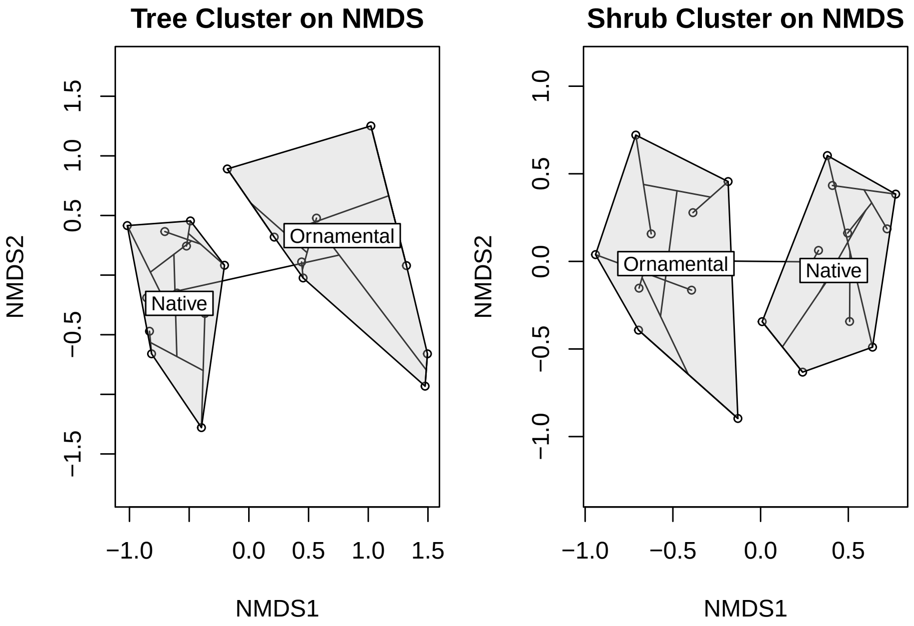

Figure 2.6: Tree and shrub community typology dendrograms plotted on NMDS. NMDS has not been rotated.

ative coefficients of 0.871 and 0.772 respectively). The native tree community typology is characterized by western red cedar, big leaf maple, Pacific madrone (*Arbutus menziesii*), and red alder (*Alnus rubra*). The ornamental tree group is characterized by red maple (*Acer rubrum*; Figure 2.6). The native shrub group is characterized by *Acer circinatum*, *Corylus sp.*, *Gaultheria shallon*, *Mahonia sp.*, *Symphoricarpos sp.*, and *Vaccinium parvifolium*; the ornamental group by *Prunus laurocerasus*. The differences between these groups based on cluster analysis and species characterization via indicator species analysis provides supports my first hypothesis of heterogeneity within the commercial land use. Dominant species for each group can be found in Appendix A: Vegetation. There is also substantial overlap between tree and shrub cluster membership. Nine sites belong to both native tree and shrub community typologies and seven sites belong to both ornamental tree and shrub community typologies, with four sites intermediate.

These typologies should better reflect vegetation on sampled sites than the pre-site selection visual inspections because they are derived from tree and shrub census data. If the observed proportions hold, I would expect 70 developments with the native tree community cluster, 335 sites with the ornamental tree community cluster, 152 sites with the native shrub community cluster, and 253 sites

Table 2.5: Category overlap between visually estimated vegetation class and flexible-beta clustering derived native/ornamental community typologies for trees. LL = low vegetation; MM = medium vegetation; MD = medium w/diverse shrubs; MC = medium w/canopy cover; HH = high vegetation

| Tree Cluster | LL | MM | MD | MC | HH |
|---|---|---|---|---|---|
| Native | 1 | 0 | 2 | 3 | 5 |
| Ornamental | 4 | 3 | 2 | 0 | 0 |

Table 2.6: Category overlap between visually estimated vegetation class and flexible-beta clustering derived native/ornamental community typologies for shrubs.

| Shrub Cluster | LL | MM | MD | MC | HH |
|---|---|---|---|---|---|
| Native | 0 | 1 | 3 | 2 | 5 |
| Ornamental | 5 | 2 | 1 | 1 | 0 |

with the ornamental shrub community cluster (Table 2.5 and Table 2.6). That is, across Bellevue and Redmond I expect approximately 1 in 5 office developments might belong to the native tree community cluster, while approximately 2 in 5 office developments might belong to the native shrub community cluster These estimates emphasize the relative rarity of the native typologies and the relative dominance of ornamental trees and shrub species, which is driven by the relative rarity of high vegetation and medium canopy groups compared with the medium vegetation group. The accuracy of these estimates will be influenced by the actual vegetation of sites assigned to the medium vegetation group, because it is the largest group and proportionally undersampled.

### 2.3.2 Explaining variation in tree and shrub community structure

Community cluster group membership represents a substantial improvement in model over vegetation class assignment in explaining variation in the surveyed tree community. None of the neighborhood socio-economic variables found significant in residential land use research were significant, nor were parcel-scale variables including those available for commercial land use, nor were maintenance variables.

NMDS plots show that variables describing the outcome of development and landscaping decisions (median Douglas-fir height, native conifer density, and presence of stands predating development) are associated with the first NMDS axis for the tree community.

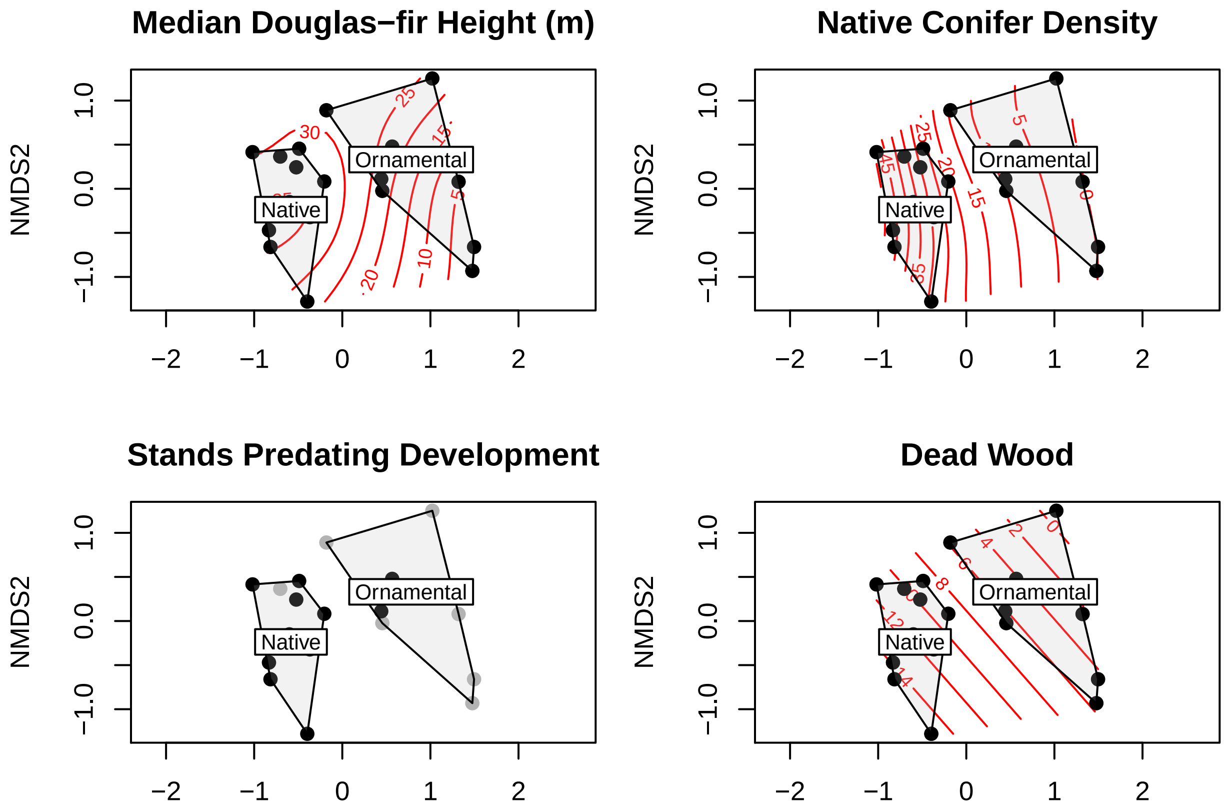

Figure 2.7: Two dimensional NMDS representation of tree community composition. Median Douglas-fir height, native conifer density, and presence of stands predating development are associated with the first NMDS axis. Dead wood is associated with both axes. Black dots represent sites with stands predating development, gray dots sites without. Ordination has not been rotated prior to plotting.

Table 2.7: PERMANOVA model summary comparing multivariate models of shrub community composition.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Tree Group Membership | 0.15 | 3.10 | 0.003 | 0.176 |
| Median Douglas Fir Height (m) | 0.15 | 3.29 | 0.002 | 0.000 |
| Stands Predate Development | 0.12 | 2.35 | 0.016 | 0.902 |
| Native Conifer Density | 0.14 | 2.98 | 0.003 | 0.294 |
| Tree Group + Median DF Height (m) | 0.23 | 2.60 | 0.001 | 0.812 |
| Tree Group + Stands Predate Development | 0.19 | 1.94 | 0.005 | 2.048 |
| Tree Group + Native Conifer Density | 0.19 | 1.99 | 0.006 | 1.942 |
| Median DF Height (m) + Stands Predate Development | 0.21 | 2.31 | 0.001 | 1.342 |
| Median DF Height (m) + Native Conifer Density | 0.22 | 2.39 | 0.001 | 1.195 |
| Stands Predate Development + Native Conifer Density | 0.18 | 1.88 | 0.012 | 2.150 |
| Median Household Income ($) | 0.07 | 1.31 | 0.178 | 1.948 |
| Shrub Cluster Name | 0.22 | 4.94 | 0.001 | 0.000 |
| Vegetation Class | 0.34 | 1.90 | 0.003 | 6.221 |

Community cluster membership also represented a substantial improvement over vegetation class assignment for the surveyed shrub community ($p$-value = 0.001 vs. 0.003). As with the tree community, none of the neighborhood socio-economic variables found significant in residential land use research were significant, nor were parcel-scale variables including those available for commercial land use, nor were maintenance variables. Variables describing the outcome of developers' actions in preserving the tree community did significantly explain variability in shrub community structure. Tree community cluster membership was also significant, consistent with the observed overlap in tree and shrub typologies. The best supported model included tree group membership and median Douglas-fir height, though other single variable PERMANOVA models and multiple two variable models received equal support (Table 2.7). The best model explained 33.674% of variation in shrub community composition.

There was no relationship between site ground cover and tree community composition (r = 0.085

and $p$-value = 0.2; Mantel on Bray-Curtis distance matrices) or shrub community composition (r = 0.085 and $p$-value = 0.056; Mantel on Bray-Curtis distance matrices).

These results suggest four patterns of particular interest. First, the age of the site was not a significant explanatory variable for tree or shrub community composition, and does not support my hypothesis that site age explains variation in vegetation community. This result is unexpected as it contradicts studies on residential properties (Avolio et al., 2018; Boone et al., 2010), the professional knowledge of landscaping professionals I interviewed, and my examination of contemporaneous landscaping plans filed with the cities of Bellevue and Redmond. A number of landscaping professionals mentioned trends in plant popularity. For example, Japanese pieris (*Pieris japonica*) was very popular in the late 1980s, while native plants have risen in popularity since 2000. There are multiple possible alternative explanations for this finding: building age may be a poor measure for landscaping age due to replanting; there may be an interaction effect between age and landscaping budget at the time of development; or only a subset of office developments may be planted with trendy landscape plants.

Second, site- and neighborhood-scale socio-economic variables were not significant in explaining variation in tree or shrub community composition. This confirms my second hypothesis that neighborhood socio-economic variables specific to residential property, including demographic variables, are not important for commercial properties. However it is surprising that site-scale socio-economic variables applicable to commercial property including building quality (a measure of rent that can be extracted) and assessed land value (a measure of land rent gradient) were not significant, disproving my third hypothesis.

For socio-economic variables to be significant drivers of vegetation on office developments, the surrounding socio-economic context would need to influence developer and landowner choices of trees and shrubs. This could occur in areas where office developments are adjacent and visible to residential property. However, the predominant development pattern in Bellevue and Redmond—and throughout the United States—is for zoning to actively separate and screen different land uses from one another. More important is likely who the intended audience of the property is, as homeowners are signaling to their neighbors while office developments are signaling to prospective and existing tenants (Cook et al., 2012; Laverne et al., 2003; Nassauer et al., 2009). Urban ecologists need to collaborate with other fields, including real estate, to develop better coupled socio-economic and ecological models for the relationship between vegetation and land use. These may include what group currently manages an office development, whether it is tenant owned or leased, and for whom the property was originally developed. For these variables and site age, a larger sample size and inclusions of variables grounded in economic theory is needed.

Third, variables describing tree preservation during development were related to tree community composition and explained variation in shrub community composition, confirming my hypothesis that the outcome of development and landscaping actions impacted vegetation communities on office developments. Tree preservation appears particularly important. This matches clustering results and suggests that a suite of decisions is being made either to retain more trees and plant native shrubs or retain fewer trees and plant ornamental trees and shrubs.

Finally, variables describing maintenance actions were not significant in explaining variation in tree or shrub community composition. I expected sites with more native trees and shrubs to be less likely to use chemical applications and those with more ornamental trees and shrub species to be more likely to use chemical applications. The amount of product may be more important, or I may not have had enough variation in maintenance regime—as evidenced by the majority of sites using some form of irrigation. Collaboration with landscape management professionals is important, as there is likely a standard maintenance regime applied at most sites.

### 2.3.3 Variation in office development vegetation communities and implications for sampling design

If urban land uses are homogeneous, we should expect to see very little variation in vegetation communities either within or between land uses. However, I observed distinct native and ornamental planting typologies within office developments, and vegetation community composition on office developments was driven by a different set of drivers than previously studied land uses. The observed heterogeneity has important implications for future research.

### Within land use variation

My clustering results show that there can be substantial variability in vegetation communities within a single land use type, here office developments, and that native planting typologies and particularly native tree typologies are much more rare than ornamental non-native typologies. This finding has important sampling design implications for researchers comparing different land uses, examining one land use across the urban gradient, or otherwise drawing conclusions about ecosystem patterns and processes in urban areas (e.g. Blair, 1999; Bourne and Conway, 2014a). Consider a small random sample of the entire population of office developments in Bellevue and Redmond. This sample would most likely contain all or almost all sites dominated by ornamental trees—as they are the most abundant in the population—with a lower chance of sampling the very different ecological communities found on native tree sites (Dyson, 2019a). As a result, this sample could lead to misleading conclusions about differences between land uses based on incomplete information and deceptively narrow standard deviations about the mean.

Researchers should therefore choose their sampling strategy carefully based on research questions and be very explicit about the limits of generalizability. Researchers should also recognize that assuming a small number of sites represent the entire land use is potentially dangerous and may lead to incorrect conclusions (McIntyre et al., 2000). Understanding the underlying variability in vegetation communities within land uses is critical to our understanding and interpretation of ecological differences in studies comparing land uses and for studies of higher trophic levels in urban environments. Particularly if you think your phenomena is related to vegetation cover/community composition, you must search out sites representing all vegetation types to measure the entire gradient. Collecting information, including visual estimation, of different types of vegetation communities on your land use prior to sampling can help improve your study's sampling design. For example, some studies have sampled based on native/non-native planting aesthetics based on knowledge of local landscaping patterns (e.g. Lerman and Warren, 2011).

### Between land use variation

Unlike similar studies on residential land uses, neighborhood socio-economic variables were not important predictors of tree or shrub community composition on commercial office developments (Clarke et al., 2013; Fraser et al., 2000; Hope et al., 2003; Luck et al., 2009; Martin et al., 2004; Schmid, 1975). My results suggest that different land use types are related differently to the same neighborhood socio-economic variables; this pattern is evident particularly when combined with the difference in explanatory power of socio-economic variables in municipal parks and office developments compared with residential land uses (Kinzig et al., 2005; Martin et al., 2004). It is likely that different motivations and preferences underlie human action impacting the vegetation community on commercial office developments when compared with residential land uses (Faeth et al., 2011; Leong et al., 2018).

The mismatch in vegetation community response to specific socio-economic drivers means that urban ecologists cannot assume that the same variables explain variation for all land use types equally. Each land use type may need to be modeled independently, and modeling all land uses within a city is likely inaccurate if you assume all land uses respond equivalently. Commercial developers and landowners are likely driven by different motivations, including ease of construction based on site conditions, cost, and development regulations. Studies examining why landscape architects make planting decisions are fewer in number than residential homeowners. In Toronto, factors like site aspect, appearance, and available space rate more highly in species selection than whether species are native and nearby canopy composition for landscape architects, however city staff try to plant native species whenever possible (Conway, 2016). Whether similar patterns hold true in the Pacific Northwest is unknown.

Studies are needed that use a paired plot design to examine the vegetation gradient in neighboring land uses with similar socio-economic contexts (e.g. adjacent industrial, residential, commercial) to compare how different land uses respond to the same socio-economic context. This should be coupled with research with components to address the what and why of different land user's motivations.

### 2.3.4 Study limitations

As with most urban ecology research, my relatively small sample size of 20 office developments creates power and other statistical barriers. However, limiting my sample size allowed me to collect a rich dataset including multiple taxonomic groups over and coordinate visits with property owners over 11-15 site visits. To include more sites, a larger team of scientists is required.

The complex nature of social-ecological systems require sampling along multiple possibly correlated gradients, including socio-economic variation (e.g. development age) and ecological variation (as here, with vegetation communities). Many studies in urban ecology implicitly sample along the socio-economic gradient by sampling along the urban or density gradient. Stratifying along the vegetation gradient of office developments allowed me to uncover a number of important trends (Dyson, 2019a, 2019b). Without this approach, I would not have been able to quantify the breadth of different vegetation typologies within one land use. However, using disproportionate stratified random sampling led to under sampling vegetation types in the “medium vegetation” category. Limiting my sampling design with respect to surrounding impervious surface and site area reduced my ability to detect the influence of these variables on vegetation community composition.

Further, my research design makes it difficult to compare with other studies. Other studies frequently use species richness and other index response variables with univariate regression instead of using multivariate regression (e.g. Hope et al., 2003; Martin et al., 2004); these measures are often dependent on effort and other factors (e.g. compare Karlik and Winer, 2001; with Martin et al., 2004). Vegetation research frequently uses a plot or transect design (Bourne and Conway, 2014a). I instead used a plotless design where the unit of analysis matched the management unit. This design allowed me to answer research questions concerning development, landscaping, and maintenance actions; transects confound different management regimes (Dyson et al., 2018).

## 2.4 Conclusions and future research directions

Human actions during development and landscaping meaningfully influence patterns of urban vegetation community composition. I observed distinct native and ornamental planting typologies within office developments resulting from tree preservation choices made during development and plant choice when landscaping (Faeth et al., 2011). Tree community composition was associated with and shrub community composition was significantly explained by development and landscaping actions resulting in older, larger native conifers being present on site. socio-economic variables found significant on other land uses were not important explanatory variables for vegetation communities on office developments. My results show that there is variability in vegetation communities both within office developments and between office developments and other land uses.

While this research finds that the observable impacts of development and landscaping actions influence vegetation community composition, the human actions leading to what is currently observable are far more complex than represented here. For example, on one sampled property about a dozen large Douglas-fir were preserved during development, but were cut down by the landowner in the following 10-15 years. On other office developments, initial plantings of ornamental shrubs were replanted to be more ecologically conscious (native species, low water use). This research left developer's and landowner's motivations as a black box, and included a limited set of independent variables describing specific outcomes of their collective actions. Without a better understanding of developer and property owner motivations, our ability to interpret the vegetation community clusters is limited, as is our ability to make policy recommendations.

Additional studies using joint socio-ecological research frameworks are needed to examine multiple factors driving decision-making, including development codes, previous land use, designer's aesthetic preferences, and explicit decisions made by the initial commercial site developers, possibly influenced by customer specifications, profit, costs, and previous experience or company aesthetic (Conway, 2016; Dorney et al., 1984; Häkkinen and Belloni, 2011; Nappi-Choulet, 2006). These include interviews with developers, landscape architects, landowners, and others to better understand tree preservation and planting motivations (Conway, 2016; Häkkinen and Belloni, 2011); aesthetic preference studies as on residential developments (Harris et al., 2012; Larson et al., 2009); tracing decision making pathways based on previous land use (Yang et al., 2017); and expanding on this research to better capture various maintenance regimes.

There are also significant opportunities for research linking together human action, ecosystem processes, urban vegetation, and higher trophic levels (Dyson, 2019a; Narango et al., 2017). Research on urban plant communities is generally restricted to one specific land use—within parks, remnant forest patches, residential neighborhoods, and occasionally vacant properties and street trees—and it is unknown how far the results of these studies can be generalized to other land use types including office developments (Bourne and Conway, 2014a). Expanding this research to encompass the whole range of urban land use types, as well as investigating the mechanistic links between landscape patterns and processes at both site- and landscape-scales are areas for potential future research. The motivations and preferences driving human action on different land uses also need to be better understood.

# Chapter 3

# Bird community on office developments is explained by development and landscaping actions impacting vegetation communities

## 3.1 Introduction

Human actions including development, tree removal, creation of impervious surface, and landscaping choices influence vegetation communities in social-ecological systems (Faeth et al., 2011). Habitat loss and degradation are primary drivers of extinction in anthropogenic habitat (Alberti, 2005; Polasky et al., 2005; Rosenzweig, 2003). For conservation efforts to be successful in social-ecological systems, the habitat matrix in which preserves and remnant habitat are situated must provide sufficient resources for local species (Fahrig, 2001; Fischer et al., 2006; Miller and Hobbs, 2002; Polasky et al., 2005; Rosenzweig, 2003; Shoffner et al., 2018). A better understanding of the relationship between bird communities and the habitat or vegetation outcomes of human action at the parcel-scale can help guide policy and management best practices to improve matrix habitat quality (Goddard et al., 2010; Miller and Hobbs, 2002).

How bird habitat use and vegetation association are impacted by development, landscaping, and management actions at the parcel-scale is one important aspect of this relationship. While human actions can control the community composition of flora, habitat selection in mobile fauna like birds results from a hierarchical processes of behavioral responses and differential habitat exploitation to increase survival (Chalfoun and Martin, 2007; Faeth et al., 2011; Hutto, 1985; McGarigal et al., 2016). Habitat use is determined by species' habitat selection process and adaptability, the spatial layout of habitat in the landscape, habitat availability and quality, and the local species pool (Cody, 1985; Müller et al., 2013).

Development actions are disturbances, and include removing vegetation and topsoil and compacting soil with heavy equipment, while landscaping actions partly replace succession processes and include choosing and planting tree and shrub species in specified proportions and locations (Grimm et al., 2017; Niinemets and Peñuelas, 2008). The resulting vegetation community composition and structure is an important component of bird habitat quality almost entirely driven by humans (Hamer and McDonnell, 2008; Heezik et al., 2012; Lepczyk et al., 2004; Müller et al., 2013; Nudds, 1977). On office developments, this range in habitats is broad, including both properties with few ornamental non-native deciduous trees planted after development and those with second growth native conifer forests preserved through development (Dyson, 2019c). Previous research suggests that bird habitat use is variably influenced by the resulting vegetation community composition. Native birds frequently prefer to feed in native trees and foliage, and sites with native plantings are more likely to retain native bird species (Belaire et al., 2014; Chace and Walsh, 2006; Chong et al., 2014; Lepczyk et al., 2004; Paker et al., 2014; Pennington and Blair, 2011). However, some native bird species are more adaptable and will readily use non-native ornamental vegetation (Belaire et al., 2014; Daniels and Kirkpatrick, 2006b).

In addition to community composition, the structure of plantings is also important (Betts et al., 2013; Jones et al., 2012; MacArthur and MacArthur, 1961; Paker et al., 2014). Bird abundance, and particularly the abundance of leaf-gleaning insectivorous species, is reduced in forest stands where vegetation structure is artificially simplified (Betts et al., 2013; Ellis et al., 2012). Heterogenous plant layers are positively correlated with high bird diversity and native forest birds (Beissinger and Osborne, 1982; Chong et al., 2014; Cooke et al., 2002, 2002; Daniels and Kirkpatrick, 2006b; Evans et al., 2009; Kroll et al., 2014; Melles et al., 2003; Paker et al., 2014; Pennington and Blair, 2011; Smith et al., 2015). Large lawns and monoculture woods without underbrush are favorable for alien bird species and urban exploiters (Paker et al., 2014; Smith et al., 2015). One potential contributing factor to this pattern is that ground cover and increased vegetation structural complexity are frequently associated with increased abundance and diversity of arthropods (Frampton et al., 2000).

Management actions, including cleanup actions, fertilization and irrigation, and pesticide application can also affect bird habitat use and bird populations in social-ecological systems. Cleanup removes dead wood and other organic matter that may function as refugia and important habitat structures (Hallett et al., 2001; Kroll et al., 2012; Linden et al., 2012). Birds that are dependent on snags for nesting, roosting, and foraging are unsurprisingly more abundant when these structures are present (Kroll et al., 2014; Linden et al., 2012; Melles et al., 2003; Sandström et al., 2006; Walter and Maguire, 2005). Nutrient addition through fertilization negatively influences bird species richness (Solomou and Sfougaris, 2015) and may alter bird habitat through changes in primary productivity, vegetation structure (habitat), and food supply i.e. invertebrate abundance (Lepczyk et al., 2004). Irrigation may increase food abundance and cover availability and drive change in bird species composition (De Frutos et al., 2015; Frampton et al., 2000; Schleder, 2010). In urban contexts, higher diversity and abundance is associated with more heavily irrigated land uses, including mesic residential yards in desert ecosystems (Cook and Faeth, 2006). Irrigated urban land uses also have higher vegetation biomass and system productivity, which may drive changes in arthropod communities (Cook and Faeth, 2006; Frampton et al., 2000; Kirchner, 1977; Shochat et al., 2004). Pesticides, including insecticides and herbicides, may impact bird populations through direct impacts (toxicity) and indirect impacts including changes in food supply and habitat (Burghardt et al., 2009; Carson, 1962; Fry, 1995; Geiger et al., 2010; Gibbons et al., 2015; Hanberry et al., 2012; Henny, 1972; Lepczyk et al., 2004; Mineau and Whiteside, 2013).

However, this previous research frequently focuses on broad neighborhood-scale vegetation patterns instead of the outcome of development, landscaping, and management actions at the parcel-scale. For example, measures of vegetation at a broad scale in bird studies include aggregate vegetation cover and distance between study site and native habitat fragments (Villegas and Garitano-Zavala, 2010). Vegetation is sometimes quantified indirectly as a function of urban form via urban gradients rather than as a result of developer and property owner actions like tree retention or landscaping (Ramalho and Hobbs, 2012). Additionally, researchers frequently conflate multiple management regimes on different parcels by aggregating vegetation information within a buffer around a point count (Clergeau et al., 1998; Lerman and Warren, 2011; Loss et al., 2009).

Results from studies using more aggregation can be difficult to interpret ecologically (McDonnell and Hahs, 2008; Ramalho and Hobbs, 2012), and results are of limited use to improve urban biodiversity outcomes through changes in human action (McDonnell and Hahs, 2013; Ramalho and Hobbs, 2012). Studies examining residential parcel-scale decisions and actions find that managed vegetation structure is an important predictor of vertebrate abundance and diversity (Daniels and Kirkpatrick, 2006b; Goddard et al., 2010). These studies provide important management information including specific actions for homeowners to take.

Here, I expand this research to commercial property. I address three questions concerning bird community composition and foraging on office developments:

1. Which bird species exhibit habitat associations with Native or Ornamental tree and shrub community typologies observed on office developments?
2. What variables describing socio-economic or land cover patterns or variables describing the outcome of development, landscaping, or maintenance actions explain variation in bird effective species richness or bird guild richness?
3. What variables describing socio-economic or land cover patterns or variables describing the outcome of development, landscaping, or maintenance actions explain variation in bird community composition and foraging bird community composition?

As highly mobile species sensitive to variation in vegetation, birds have been used as indicators of biodiversity globally and in urban ecosystems, and patterns of bird habitat use may provide information on the resources available to other trophic levels at an office development (Blair, 1999; Butchart et al., 2010; Croci et al., 2008). Birds are also charismatic, and provide cultural ecosystem services important to large numbers of citizens (Collins et al., 2011; Whelan et al., 2015; White et al., 2018). These characteristics make them an ideal study species to examine the impacts of human development, landscaping, and management actions determining vegetation at the parcel-scale on higher trophic organisms.

I compared vegetation communities on office developments with the community composition of birds and the subset of birds engaged foraging behavior (foraging birds) observed on each site during the winter. Winter bird communities are less well studied than breeding bird communities (Jokimäki and Kaisanlahti-Jokimäki, 2003). Resources obtained during the winter season are critical for survival and impact body condition for migration and reproduction. Thus, the winter season may help shape resident (year-round) bird communities and contribute significantly to population dynamics (Devries et al., 2008; Faaborg et al., 2010; Manuwal and Huff, 1987; Marra et al., 1998). Bird species' diets are frequently relaxed in the winter, which suggests opportunities for urban vegetation to provide birds with critical food resources (Faaborg et al., 2010; Poole, 2016).

I quantified the bird communities and observed feeding behavior on office developments, collected data on tree, shrub, and ground cover communities, gathered information about parcel- and neighborhood-scale socio-economic and land cover variables, and quantified parcel-scale outcomes of development, landscaping, and management actions. This focus on action outcomes allows me to make development and landscaping suggestions, however developer and land owner motivation is not addressed. I used cluster analysis, regression, and multivariate ecology tools including PERMANOVA to quantify the relationship between bird communities and independent variables.

I hypothesized that bird species on commercial property are associated with the same habitat as observed in non-urban systems (Poole, 2016), and that univariate (effective species richness) and multivariate (community composition) analyses would reveal different patterns. Based on previous research, I hypothesized that top-down neighborhood-scale socio-economic and land cover variables found significant in studies of residential land use types, including median household income, would be significant in explaining variation in effective species richness and community structure (Beumer and Martens, 2015; Heezik et al., 2013; Lerman and Warren, 2011; Luck et al., 2013; Melles et al., 2003; Schütz and Schulze, 2015). I also hypothesized that variables describing the outcome of development, landscaping, and management actions impacting vegetation on site would also be significant in explaining variation in the bird community (Belaire et al., 2014; Daniels and Kirkpatrick, 2006b; Galitsky and Lawler, 2015). The relative importance of neighborhood-scale "top-down" variables emerging from diffuse decisions in social-ecological systems and parcel-scale "bottom-up" variables resulting from parcel-level decision making varies by location and taxonomic group (Belaire et al., 2014; Daniels and Kirkpatrick, 2006b; Galitsky and Lawler, 2015; Kinzig et al., 2005). Previous research suggests that for birds in the Puget Trough local factors were twice as important as landscape patterns for frugivores, seed eaters, ground foragers, and bark foragers (Galitsky and Lawler, 2015). Therefore I also hypothesized that parcel-scale variables would be more important in explaining variation in bird communities than neighborhood-scale variables. A local understanding of the relative influence these factors in determining habitat use by birds is an important consideration for urban bird conservation planning and success (Kinzig et al., 2005).

Broadly, I found that birds are associated with the same habitat on office developments as observed elsewhere. I also found that parcel-scale variables are more important in explaining variation in bird communities than neighborhood-scale variables. Both bird effective species richness and bird community composition on office developments are influenced by parcel-scale development and landscaping actions, including the age and density of native trees and the density of native shrubs on a parcel. These findings suggest an important role for developers, land owners, landscape architects, and tree protection policy in bird conservation, and a need for additional research examining how land use policy is implemented at the parcel-scale, what factors influence developer and landowner actions, and how to best incentivize actions like native conifer preservation associated with more diverse winter bird communities.

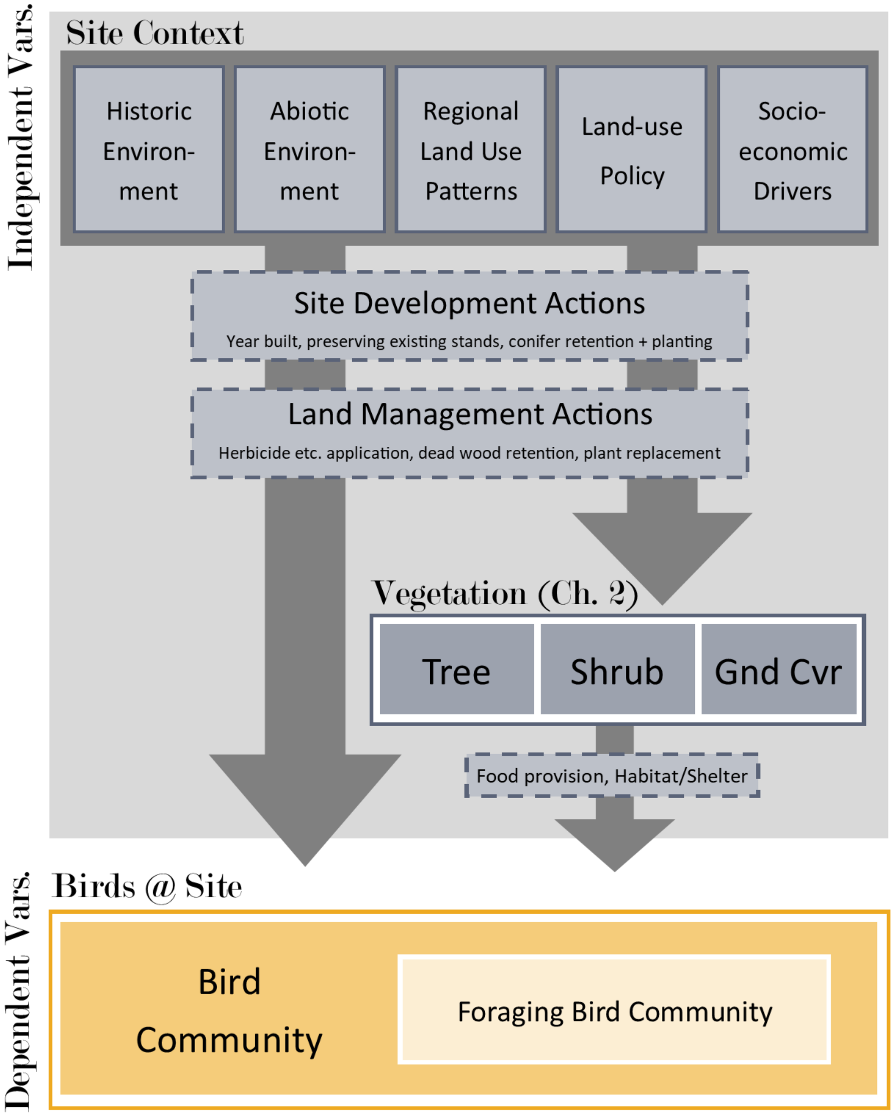

Figure 3.1: An overview of the relationships between measured variables and the bird community present at a site. When a site is developed, the developer's actions determine whether stands of trees are preserved through development, as well as the preserved conifer density, the initial planting design, and the year built. These variables are further modified by the land management actions, including herbicide/pesticide/etc. applications, dead wood removal, and plant replacement. These variables may influence bird community composition in two ways. First, the resulting vegetation on the site influences habitat available to birds. Second, a subset of these variables—such as the socio-economic variables and impervious surfaces—may influence the surrounding bird community and therefore limit the bird community at the neighborhood-scale.

## 3.2 Methods

### 3.2.1 Study area

Redmond (2017 population 64,000) and Bellevue (population 144,000) are located east of Seattle in King County, Washington in the Puget Trough region (United States Census Bureau, 2017). This temperate lowlands region lies between the Cascades and Puget Sound, with post glaciation conifer-dominated forests of Douglas-fir, western red cedar, and western hemlock (*Pseudotsuga menziesii*, *Thuja plicata*, and *Tsuga heterophylla*). Both cities share a similar ecological history including glaciation ending 10,000 years ago, a similar disturbance timeline for logging and agriculture, and have grown considerably since the opening of the Evergreen Point Floating Bridge (SR 520) in 1963. They are at similar elevations ($<$ 500 ft) and experience the same climate and weather. The two cities are approximately 20 miles from the foothills of the Cascades, and 30 miles from forested mountains $>$ 4,000 ft elevation. Two large lakes, Lake Washington and Lake Sammamish, are adjacent to city borders.

Study sites were selected using disproportionate stratified random sampling across five vegetation strata to ensure that my sample included sites across the entire vegetation gradient (Dyson, 2019c). The sampling frame was limited to Redmond and Bellevue north of I-90 and excluded developments in Bellevue's central business district. To avoid confounding factors, I restricted the sampling pool to sites in the 25th to 85th percentile for size and the 15th to 85th percentile for surrounding impervious surfaces.

I sent three rounds of mailings to the property owner or manager on file in the King County Assessor's database published October 9th, 2014, requesting access to their property (Dyson et al., 2018). Twenty of the 46 requests sent were accepted, 6 requests were rejected, and 20 received no response or were not deliverable. My final sample included 3-5 sites from each of the five vegetation strata, with 13 sites were located in Bellevue and 7 of the study sites were located in Redmond. The study sites ranged from 0.631 acres to 5.39 acres in size. The office developments on study sites were built between 1975 and 2008. Commercial use of the sites included light industrial, white collar office space, medical/dental offices. Some sites were fully leased to tenants, while others were either partly or fully owner-occupied. Company size ranged from one to many thousand employees.

### 3.2.2 Bird surveys

I conducted bird surveys between December 12th 2014 and March 1st 2015 and between December 11th 2015 and February 27th 2016. Sampling occurred on days when wind speed was less than 10 mph and rainfall was less than 0.1". I delayed sampling when there was thick fog in the early morning, however light rain and fog are normal winter conditions. I conducted 40 days of sampling per year comprising four rounds of surveys for each of 20 sites to reduce winter weather bias and characterize bird communities (Marzluff et al., 2016). Two sites were visited per day. Sweeps at the first site began at sunrise (approx. 8:00 AM) and sweeps at the second site finished between 10:00AM and 1:00PM due to the variable sampling length and between site transit times. Site visit order was randomized for each round of surveys, and were visited in this order except when scheduling conflicts arose with the property owner or manager. While these scheduling constraints may introduce bias, they are an unavoidable when working on private property (Dyson et al., 2018).

Birds were surveyed using the standardized search method (Watson, 2003). The standardized search method allows for comparison of heterogeneous study sites, retains the parcel as the unit of analysis instead of changing it to the point count circle, and is compatible with the geometry of parcels (Dyson, 2019c; Watson, 2003). The method encourages observer movement, which allowed for detection of cryptic winter species, observation of bird behavior and foraging activity, and repositioning to mitigate the impacts of urban noise. Pilot data collected using both point count and standardized search methodology confirmed the superiority of the standardized search methodology in detecting birds (Dyson, unpublished data).

During each site visit, 20-minute sweeps were conducted consecutively until the stopping rule was met, here no new species observed in the sweep. This resulted in 2–7 sweeps per visit with a median of 4 sweeps per visit. I recorded each bird species along with detection method, whether birds were foraging, and location on site. Foraging activities required visual confirmation except for woodpeckers. I did not estimate abundance or record birds flying overhead, water dependent birds, or raptors, following Melles et al. (2003) and Jokimäki and Suhonen (1998). Each sweep was recorded using an Olympus WS-822 digital voice recorder. Recordings were used to confirm identifications made in the field and perform quality checks by Bob Sundstrom and myself.

### 3.2.3 Bird guilds

I constructed bird guilds based on the Birds of North America Online database and classified bird species based on three factors: diet, foraging substrate, and forest preference (Poole, 2016). I used three diet categories: insectivore (90%+ insects), grainivore (90%+ seeds), omnivore (mix of insects/invertebrates, fruit, seeds, and other plant parts in various proportions). The three foraging substrate classes were: ground foragers, tree and shrub foragers, or no preference; the no preference group was not analyzed as it contained only 3 bird species. I used three forest preference classes: conifer, mixed conifer/deciduous, and no preference or open habitat preferred.

I chose these groups based on previous research examining the impact of urbanization on bird trophic guilds. Most studies on feeding guilds focus on diet, including granivores (Blair and Johnson, 2008; Chace and Walsh, 2006; Werner and Zahner, 2009; Zhou and Chu, 2012), omnivores (Jokimäki and Kaisanlahti-Jokimäki, 2003; Lepczyk et al., 2004), and insectivores (Beissinger and Osborne, 1982; Blair and Johnson, 2008; Chace and Walsh, 2006; Zhou and Chu, 2012). Changes in vegetation structure and composition also impact richness of bird guilds defined by foraging method. In urban areas, canopy and bark gleaners are reduced while ground gleaners are more abundant (Beissinger and Osborne, 1982; Chace and Walsh, 2006).

### 3.2.4 Independent variables

#### Detection variables

Potential detection variables include noise levels and weather conditions that can influence the observer's ability to detect birds. Loud noise conditions were recorded in situ and when they consistently interfered with detection, such as leaf blower noise from adjacent property (Leukering et al., 1998). Overcast skies (76-100% cloud cover), fog, and drizzle were also recorded. Hourly data for air temperature, rainfall, wind speed, and solar radiation (brightness) were obtained from AgWeatherNet and the median across time spent at each site calculated (Woodinville sensor; Ag-WeatgerNet Team, Washington State University, 2016).

### Vegetation data

**Tree Community:** At each site, individual trees > 4" DBH were identified to species or genus (Cope, 2001; Dirr, 2009, 1997; Schoon, 2011; Sibley and others, 2009; Symonds, 1958). Flexible beta clustering and indicator species analysis identified two tree community typologies on office developments, characterized by native and ornamental species. Other variables derived from the tree community include median dominant Douglas-fir height as a proxy for tree age and native conifer density. The presence of stands predating development was determined from historical records (Dyson, 2019c).

**Shrub Community:** At each site, all members of the shrub community were identified to species or genus (Brenzel, 1995; Dirr, 2009, 1997; Krüssmann and Warda, 1985; Symonds, 1963). Flexible beta clustering and indicator species analysis were used to identify two shrub community typologies, as with the tree community they were characterized by native and ornamental species respectively. Other variables derived from the shrub community include the density of native shrubs and effective species richness of native shrub species (Jost, 2006). Tree and shrub genera were assigned to one of three provenance categories—native, non-native, or ambiguous—based on range information from the United States Geological Survey and the United States Department of Agriculture (U.S. Geological Survey, 1999; USDA, 2016). The ambiguous category was used for genera including both native and non-native cultivated species that are difficult to distinguish, and/or frequently interbred and sold as crosses.

**Ground Cover:** Ground cover types were recorded on paper maps, then hand digitized to calculate the area of impervious surfaces on site (QGIS Development Team, 2016).

Table 3.1: Definition of independent variables used in bird community analysis.

| Variable Name | Definition | Data Source |
|---|---|---|
| **1.** | **DETECTION VARIABLES** | |
| **Loud Noise (% visits)** | Proportion of site visits with loud noise. | Site survey |
| **Fog (% visits)** | Proportion of site visits with fog. | Site survey |
| **Light Rain (% visits)** | Proportion of site visits with light rain. | Site survey |
| **Overcast (% visits)** | Proportion of site visits where cloud cover exceeded 75%. | Site survey |
| **Median Air Temperature (F)** | Median of median air temperature observed during each visit. | WSU AgWeatherNet |
| **Median Wind Speed (MPH)** | Median of median wind speed observed during each visit. | WSU AgWeatherNet |
| **Median Wind Gust (MPH)** | Median of median wind gusts observed during each visit. | WSU AgWeatherNet |
| **Total Precipitation (inches)** | Summed over all 8 visits. | WSU AgWeatherNet |
| **Median Solar Radiation (W/m^2)** | Median of median solar radiation observed during each visit. | WSU AgWeatherNet |
| **2.** | **VEGETATION GROUPS** | |
| **Tree Community Group** | Broad tree community typology (native or ornamental) based on flexible beta cluster analysis of tree density data. | Site survey |
| **Shrub Community Group** | Broad shrub community typology (native or ornamental) based on flexible beta cluster analysis of shrub density data. | Site survey |
| **3.** | **SITE-SCALE SOCIO-ECONOMIC VARIABLES** | |
| **Area** | Site area, in acres. | King County Assessor |
| **Town** | Location, Bellevue or Redmond. | King County Assessor |
| **Building Age (in 2017)** | Age of building on site (or mean age for multiple buildings) in 2017. | King County Assessor |
| **Building Quality** | Categorical quality class assigned to buildings on the parcel. | King County Assessor |
| **Appraised Land Value per Acre** | Appraised land value divided by site area. One missing assessed land value was replaced with the population median land value. | King County Assessor |
| **4.** | **NEIGHBORHOOD LAND COVER AND SOCIO-ECONOMIC VARIABLES** | |
| **Impervious w/in 500 m (%)** | Percent of impervious surface within 500 m of the site's perimeter. | National Land Cover Database 2011 Percent Developed Imperviousness dataset updated in 2014 |

| | | |
|---|---|---|
| **Tall Vegetation w/in 500 m (%)** | Percent of tall tree vegetation canopy cover within 500 m of the site's perimeter. | NDVI calculated using the 2015 NAIP data and object height calculated using 2014 and 2013 LiDAR data |
| **Short and Medium Vegetation w/in 500 m (%)** | Percent of short and medium vegetation canopy cover within 500 m of the site's perimeter. | NDVI calculated using the 2015 NAIP data and object height calculated using 2014 and 2016 LiDAR data |
| **Major intersections w/in 500 m (count)** | Number of major intersections located within 500 m of the site's perimeter. | OpenStreetMap |
| **Median Income** | The median income of residents for the site's block group. | American Community Survey 2014 5-year block group |
| **Percent Foreign-Born** | The percent of residents born outside of the United States for the site's block group. | American Community Survey 2014 5-year block group |
| **5.** | **DEVELOPMENT, LANDSCAPING, AND MAINTENANCE VARIABLES** | |
| **Impervious on Site (%)** | Percent of the parcel's area occupied by impervious surface. (Development) | Site survey |
| **Stands Predate Development** | Presence/absence of a stand of three+ trees nearby one another that predate development. (Development) | Site survey |
| **Median Height of Dominant Douglas-fir** | Median height (m) of 5 dominant Douglas-fir, as a proxy for age. (Development) | Site survey |
| **Density of Native Conifers** | Total density of Douglas-fir, western red cedar, and western hemlock. (Development/ Landscape) | Site survey |
| **Native Shrub Effective Species Richness** | Effective species richness is calculated as exp(H'), following Jost (2006). (Landscaping) | Site survey |
| **Density of Native Shrubs** | Combined density of all native shrub species (# / site area in acres). (Landscaping) | Site survey |
| **Cleanup** | Indicates whether the landscaping crew removes detritus from the site. (Maintenance) | Interviews and site survey |
| **Irrigation** | Indicates whether irrigation is used during the summer months. (Maintenance) | Interviews and site survey |
| **Mulch, Herbicide, and/or Fertilizer Application** | Variables (3) indicating whether landscaping crew applies mulch, herbicides, or fertilizers to a site. (Maintenance) | Interviews and site survey |
| **Mushroom Removal** | Indicates whether the landscaping crew removes above-ground mushrooms. (Maintenance) | Interviews and site survey |
| **Dead Wood** | Total abundance of stumps, logs, and snags on site. (Maintenance) | Site survey |

### Parcel and Neighborhood Variables

I calculated parcel-scale socio-economic variables including site area, year built, building quality, assessed land value per acre, and town, and neighborhood-scale variables including percent impervious within 500 m, median household income, and percent foreign-born based on available databases (Dyson, 2019c; Homer et al., 2015; King County Department of Assessments, 2014; King County GIS Center, 2014; United States Census Bureau, 2016; Xian et al., 2011).

Neighborhood-scale variables include measures of the built environment and socio-economic context found significant in explaining bird habitat use in previous studies (Beumer and Martens, 2015; Germaine et al., 1998; Heezik et al., 2013; Hope et al., 2003; Kinzig et al., 2005; Lerman and Warren, 2011; Loss et al., 2009; Luck et al., 2013; Melles, 2005; Munyenyembe et al., 1989; Schütz and Schulze, 2015; Villegas and Garitano-Zavala, 2010). For neighborhood variables, I chose a 500 m buffer based on previous research and the likely winter foraging ranges of local native bird species (Melles et al., 2003; Poole, 2016). In the study area, this foraging range includes multiple land use types; the commercial properties studied were often adjacent to residential property, and all properties had residential land uses within 500 m. While decisions on in social-ecological systems are driven by a diversity of human agents, and decisions on commercial properties are likely driven by different motivations and considerations than residential property, bird ranges include both types of property and this should be reflected in models. Additionally, including these variables facilitates comparison with results from residential property.

For birds, canopy cover and canopy height are measures of neighborhood vegetation used in the literature (Beumer and Martens, 2015; Heezik et al., 2013). I quantified the percent of tall tree canopy cover and of short and medium height vegetation cover using NAIP and LiDAR data and determined the number of major intersections in a 500 m radius to further measure the habitat matrix in the neighborhood surrounding each site. To calculate vegetation cover measures, I first calculated NDVI from the 2015 NAIP data (USGS, 2015). I also calculated object height from 2014 Redmond LiDAR data and 2016 King County LiDAR data by subtracting the digital terrain model from the digital surface model (Quantum Spatial, 2017, 2014). I classified pixels as tall tree canopy when NDVI $\geq 0.15$ and object height $\geq 50$ feet and as short and medium height vegetation when NDVI $\geq 0.15$ and object height $< 50$ feet. The percent cover of each was then calculated in a 500 m radius around the parcel boundary. I calculated the number of major intersections by intersecting major road data, checking for accuracy by hand, and then counting the number of intersections within a 500 m radius (OpenStreetMap Foundation, 2017).

### Maintenance data

I interviewed each site's landscaping service using the elite interview technique and supplemented these interviews with observational data from site visits (Dexter, 1970; Harvey, 2011). I then assigned a value (Yes, No, Unknown) to variables based on performance of the following maintenance activities at each site: cleanup (leaf blowing, mowing, etc.), herbicide application, fertilizer application, insecticide application, fungicide application, summer irrigation, mulch application, and mushroom removal. I removed "Insecticide" and "Fungicide" application from further consideration as there were no "Yes" responses. I chose these maintenance variables based on previous research results (Cook and Faeth, 2006; De Frutos et al., 2015; Gibbons et al., 2015; Lepczyk et al., 2004; Mineau and Whiteside, 2013; Solomou and Sfougaris, 2015).

I also censused each site for logs, snags and stumps based on existing knowledge of bird habitat preference (Hallett et al., 2001; Kroll et al., 2012; Linden et al., 2012; Walter and Maguire, 2005). Logs needed to be more than 6" in diameter for inclusion. Snags needed to be more than 6" in diameter with the majority more than 6' tall; dead wood not meeting this height requirement was considered a stump. Shrub stumps were not counted towards the total. Multi-trunk stumps were counted only once. Stumps where the tree had grown from a co-dominant trunk were counted.

## 3.2.5 Data analysis

Data analysis methods are summarized in Figure 3.2.

### Bird incidence calculation

Bird species incidence was defined as $incidence = \frac{\text{count of visits observed}}{\text{8 visits}}$. I used incidence and not a repeated measures design as between site, not between year, variability is important. Incidence also

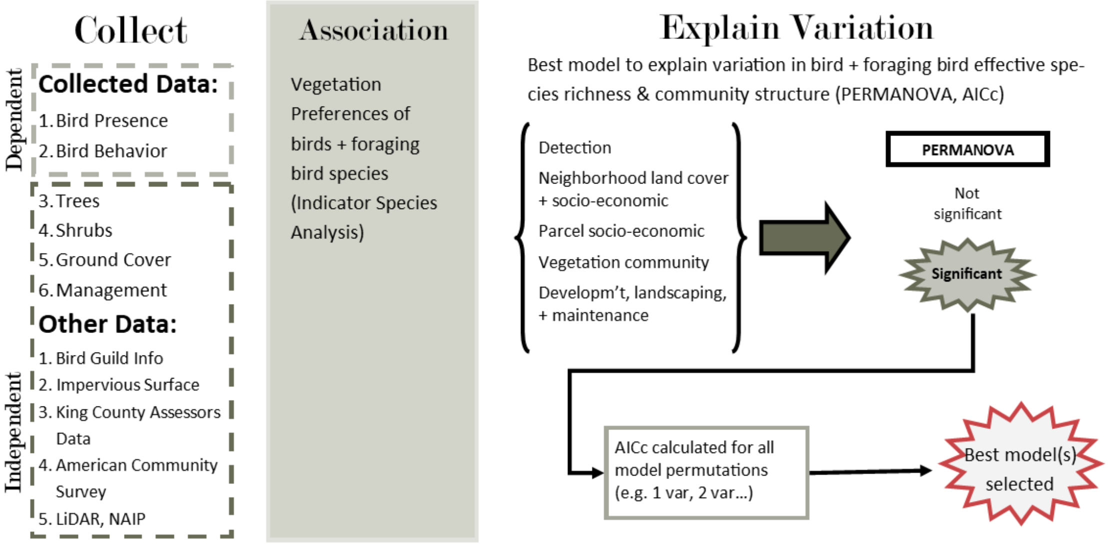

Figure 3.2: Summary of data analysis methods for bird communities.

reduces the influence of local species subject to population irruptions including Red Crossbill and Bushtit. Unknown species were recorded in the field but removed from analysis; unknown species accounted for only 13 out of 3237 observations (0.402%).

Rare species observed fewer than two times were removed prior to calculating univariate effective species richness for all birds and bird guilds (Jost, 2006). Rare species were not removed from multivariate community composition matrices (McCune et al., 2002). No further transformations (e.g. Wisconsin standardization) were used for multivariate analysis. The standardized search methodology controls appropriately for between-site variability making this transformation unnecessary.

### Vegetation association preference

Correlation indices were used to determine the ecological preferences of species, among a set of site groups with different conditions—here, native vs. ornamental tree and shrub community typologies identified using flexible-beta cluster analysis (De Cáceres, 2013b; De Cáceres et al., 2010). I used a custom wrapper for the multipatt {indicspecies} implementation of the point biserial correlation coefficient to run the function 100 times and keep indicator species present in $> 50\%$ of the runs (De Caceres and Legendre, 2009; function r.g; De Cáceres et al., 2010; Dyson, 2018). I took the mean indicator statistic and kept those species with a mean index value $> 0.5$. I took this cutoff from Hinkle et al. (2002), who suggest that correlation size 0.5-0.7 is a moderate correlation; 0.7-0.9 a high correlation, and 0.9-1.0 a very high correlation.

### Explaining variation in effective species richness

Effective species richness is defined as the exponent of Shannon entropy (Jost, 2006). To assess variation in effective species richness and partition variation, I tested each independent variable in a simple univariate model using the adonis2 {vegan} PERMANOVA implementation with the Euclidian distance matrix (Bakker et al., 2012; Oksanen et al., 2017). Significance for all tests was assessed on pseudo-$F$ $p$-values at $\alpha \leq 0.05$. I then constructed models using all significant variables without significant betadispersion in all possible single and multiple variable model combinations. I used a custom AICc function based on Residual Sums of Squares to compare models and identify those with the best support. This sequential testing and model iteration approach reduced the need to standardize independent variables or use PCA to collapse related variables. This helped ensure interpretable results that are more relevant to urban planners and management professionals.

For bird guild species richness, I used two of the most supported variables for the full community and percent impervious surface found significant in other studies. I used the Holm-Bonferroni method to control error rate within groups, and also calculated Spearman's correlation {stats}.

### Explaining variation in bird community structure

I used PERMANOVA to identify variables that explain variation in bird or foraging bird community composition and NMDS for visualization (McCune et al., 2002; Oksanen et al., 2017). As in univariate analysis, I tested each independent variable in a simple multivariate model using a Bray-Curtis distance matrix (Anderson, 2001, Oksanen et al. (2017)). I used ANOVA to test for significant differences in categorical group dispersion using anova(betadisper()) {stats} {vegan} (Oksanen et al., 2017). For variables with significant pseudo-$F$ values and non-significant betadispersion, I calculated AICc using a custom function based on Residual Sums of Squares to compare all possible models using this reduced set of variables.

## 3.3 Results

I observed 36 species during my surveys, 31 of which were observed foraging. The number of species observed on each site varied between 10 to 25 species (mean 17.9 ± 4.4), with the number of bird species observed foraging between 8 to 21 species per site (mean 15.05 ± 4.3).

The most frequently observed species included Dark-eyed Junco (83.1% of visits), American Crow (75.6% of visits), and Golden-crowned Kinglet (72.5% of visits). Common Raven, Downy Woodpecker, Hutton's Vireo, Killdeer, and Rock Pigeon were each seen only once (0.6% of visits). Most bird species I observed were native; of the three non-native species encountered, only European Starling was observed with frequency (11 sites), and House Sparrow and Rock Pigeon were seen at only 1 site each. The overall prevalence of non-native species was low compared with previous research on winter urban bird communities (Clergeau et al., 1998). Full species lists are available in Appendix B: Birds.

### 3.3.1 Vegetation association preference

Bird species associated with conifer forests, including Brown Creeper and Townsend's Warbler, prefer sites with native tree community clusters (Poole, 2016). The only bird species associated ornamental tree communities was the American Crow. The habitat preferences of birds observed foraging on site also follows this pattern (Table 3.2).

### 3.3.2 Explaining variation in effective species richness

#### Effective species richness of all observed bird species

The proportion of overcast survey visits, significantly explained variation in effective bird species richness. Three variables describing the outcome of development and management actions were

Table 3.2: Bird species with significant ecological preferences as determined by point biserial correlation.

| Bird Species | Vegetation Type | Mean Statistic | Mean Foraging Stat | Diet | Foraging Substrate | Forest Preference |
|---|---|---|---|---|---|---|
| Red-breasted Nuthatch | Native Tree | 0.756 | 0.708 | Omnivore | Trees and Shrubs | Conifer |
| Brown Creeper | Native Tree | 0.626 | 0.555 | Insectivore | Trees and Shrubs | Conifer |
| Townsend's Warbler | Native Tree | 0.510 | 0.512 | Insectivore | Trees and Shrubs | Conifer |
| Golden-crowned Kinglet | Native Tree | 0.506 | — | Insectivore | Trees and Shrubs | Conifer |
| Chestnut-backed Chickadee | Native Tree | — | 0.512 | Omnivore | Trees and Shrubs | Conifer |
| American Crow | Ornamental Tree | — | 0.554 | Omnivore | Ground | Open or No Preference |

significant after controlling for the proportion of overcast visits: presence of stands predating development, percent impervious surface on site, and median Douglas-fir height (Figure 3.3). The site's tree and shrub community typology identification as either native or ornamental was also significant. No neighborhood socio-economic variables, neighborhood land cover variables, or other landscaping and maintenance variables were significant; all single variable results can be found in Appendix B: Birds)

The best supported model includes proportion of overcast visits and median dominant Douglas-fir height, though the model with these variables and the presence of a stand predating development receives equal support (Table 3.3). No interaction terms were significant. The consistent inclusion of median Douglas-fir height in the best supported models suggests that this variable was particularly important for explaining variation in effective bird species richness. Variation explained for both models was approximately 75%.

### Effective species richness of bird guilds

Effective species richness of omnivores and insectivores were both positively correlated with presence of stands predating development and median Douglas-fir height (m) and negatively correlated with percent impervious on site, while grainivores were not correlated to any of these variables. Insectivores showed particularly high variation explained for stands predating development and median Douglas-fir height (Table 3.4). Effective species richness of birds foraging on the ground and

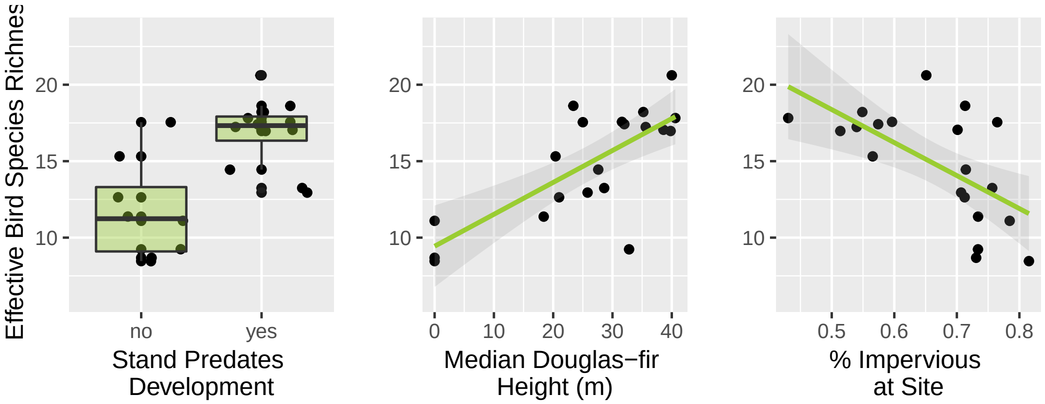

Figure 3.3: Three development and landscaping variables which significantly explain variation in bird effective species richness, with ecologically meaningful effect sizes. The presence of stands predating development was associated with a greater effective species richness of approximately 7 bird species, and for every additional 10 m median Douglas-fir height effective species richness can be expected to increase approximately 3 species. Increasing percent impervious on site by 10% can be expected to decrease effective species richness by approximately 2 species

Table 3.3: Variables that significantly explain variation in bird effective species richness. Variables were tested in simple univariate models with overcast visits used as a control variable.

| | Variation Explained | Pseudo-F | p-value | Delta AICc |
|---|---:|---:|---:|---:|
| **Median Douglas Fir Height (m)** | 0.426 | 26.790 | 0.000 | 0.000 |
| **Stand Predating Development** | 0.327 | 15.032 | 0.002 | 6.253 |
| **Tree Cluster Group** | 0.247 | 9.364 | 0.009 | 10.148 |
| **Native Conifer Density** | 0.225 | 8.096 | 0.012 | 11.134 |
| **Native Shrub Effective Richness** | 0.216 | 7.620 | 0.014 | 11.517 |
| **Native Shrub Density** | 0.205 | 7.083 | 0.018 | 11.958 |
| **On Site Impervious (%)** | 0.201 | 6.890 | 0.018 | 12.118 |
| **Shrub Cluster Group** | 0.179 | 5.875 | 0.029 | 12.987 |
| **Overcast Visits (%; Control Var)** | 0.303 | 7.835 | 0.013 | 16.130 |

in trees or shrubs was positively correlated to stands predating development and median Douglas-fir height (m) though surprisingly not with percent impervious on site (adjusted $p$-value = 0.06). Only the effective species richness of conifer-associated birds was positively correlated to stands predating development and median Douglas-fir height and negatively to percent impervious on site; birds associated with mixed forests were not correlated with any variables and birds associated with open areas or without preference were correlated only weakly with median Douglas-fir height.

Table 3.4: Percent impervious surface on site, presence of stands predating development, and median Douglas-fir height (m) explained variation in effective species richness of bird guilds (diet, foraging location, and forest preference).

| **Bird Guild** | **Stand Predates Devlp't** | **Median D-f Height (m)** | **Pct Imperv on Site** |
|---|---|---|---|
| **DIET** | | | |
| **Omnivore** | Variation Expld: 0.477<br>Adj pval: 0.005 | Correlation: 0.682<br>Variation Expld: 0.517<br>Adjusted pval: 0.0024 | Correlation: -0.75<br>Variation Expld: 0.417<br>Adjusted pval: 0.015 |
| **Insectivore** | Variation Expld: 0.71<br>Adj pval: 2e-04 | Correlation: 0.8<br>Variation Expld: 0.681<br>Adjusted pval: 1e-04 | Correlation: -0.75<br>Variation Expld: 0.473<br>Adjusted pval: 0.006 |
| **Grainivore** | Adj pval: 0.561 | Adj pval: 0.303 | Adj pval: 0.569 |
| **FORAGING LOCATION** | | | |
| **Ground** | Variation Expld: 0.389<br>Adj pval: 0.0178 | Correlation: 0.676<br>Variation Expld: 0.459<br>Adjusted pval: 0.0044 | Adj pval: 0.054 |
| **Tree and Shrub** | Variation Expld: 0.429<br>Adj pval: 0.0113 | Correlation: 0.58<br>Variation Expld: 0.408<br>Adjusted pval: 0.0103 | Adj pval: 0.062 |
| **FOREST PREFERENCE** | | | |
| **Conifer** | Variation Expld: 0.557<br>Adj pval: 0.0026 | Correlation: 0.706<br>Variation Expld: 0.482<br>Adjusted pval: 0.0044 | Correlation: -0.75<br>Variation Expld: 0.566<br>Adj pval: 0.001 |
| **Mixed** | Adj pval: 0.187 | Adj pval: 0.243 | Adj pval:0.319 |
| **Open or No Preference** | Adj pval: 0.187 | Correlation: 0.532<br>Variation Expld: 0.369<br>Adjusted pval: 0.0145 | Adj pval:0.538 |

### 3.3.3 Explaining variation in bird community structure

The proportion of overcast site visits was also a significant detection variable explaining variation in both the community composition of all birds observed and of foraging birds observed. After controlling for this, all significant variables for both communities represented the outcome of development, landscaping, and management actions. These variables describe the native tree community on site (median Douglas-fir height as a proxy for tree age, the presence of stands predating development, and native conifer density, tree community cluster), the native shrub community on site (native shrub effective species richness and for foraging birds only, native shrub density), and percent impervious surface and dead wood abundance on site (see Appendix B: Birds). None of the neighborhood- or parcel-scale socio-economic variables or neighborhood land cover variables were significant, nor were most variables describing maintenance actions (e.g. herbicide application).

The best supported model for all bird and foraging bird community composition, as with univariate models, included the proportion of visits overcast and median dominant Douglas-fir height. Multiple other models received equal support, including single variable models with percent impervious surface on site and native conifer density, and multiple two variable models. Other two and three variable models along with all four+ variable models received substantially less support (Table 3.5 and Table 3.6). The best supported models explain approximately 37-43% of variation. Median dominant Douglas-fir height and native conifer density were consistently included in models with $\Delta$ AICc $\leq 2$.

Table 3.5: Comparison of bird community PERMANOVA models using AICc. Models with socio-economic variables were not significant; median household income is presented here for comparison only.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Proportion of Visits Overcast | 0.126 | 2.604 | 0.034 | 3.743 |
| Overcast and Median DF Height (m) | 0.370 | 4.991 | 0.001 | 0.000 |
| Overcast, Median DF Height, and Native Shrub Effective Richness | 0.438 | 4.154 | 0.001 | 0.887 |
| Overcast, Impervious, and Median DF Height | 0.424 | 3.932 | 0.001 | 1.359 |
| Overcast, Native Conifer Density, and Median DF Height | 0.418 | 3.828 | 0.001 | 1.585 |
| Overcast, Tree Community Cluster, and Median DF Height | 0.413 | 3.759 | 0.001 | 1.736 |
| Overcast and Native Conifer Density | 0.312 | 3.846 | 0.003 | 1.773 |
| Overcast and Impervious (on site) | 0.311 | 3.836 | 0.001 | 1.790 |
| Overcast, Dead Wood, and Median DF Height | 0.407 | 3.664 | 0.001 | 1.946 |
| Overcast and Median HH Income ($) | 0.164 | 1.669 | 0.096 | 5.654 |

Table 3.6: Comparison of foraging bird community PERMANOVA models using AICc. Models with socio-economic variables were not significant; median household income is presented here for comparison only.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Overcast | 0.132 | 2.728 | 0.033 | 3.525 |
| Overcast and Median DF Height (m) | 0.367 | 4.925 | 0.001 | 0.000 |
| Overcast, Median DF Height, and Native Shrub Effective Richness | 0.435 | 4.112 | 0.001 | 0.877 |
| Overcast and Native Conifer Density | 0.314 | 3.882 | 0.001 | 1.617 |
| Overcast, Tree Community Cluster, and Median DF Height | 0.412 | 3.735 | 0.001 | 1.691 |
| Overcast and Stand Predates Development | 0.306 | 3.741 | 0.003 | 1.846 |
| Overcast, Stand Predates Development, and Median DF Height | 0.407 | 3.658 | 0.001 | 1.861 |
| Overcast, Median DF Height, and Dead Wood Abundance | 0.403 | 3.599 | 0.001 | 1.994 |
| Overcast and Socio-economic Variables (Median HH Income, $) | 0.157 | 1.585 | 0.103 | 5.721 |

## 3.4 Discussion

Development and landscaping actions alter vegetation communities in social-ecological systems (Avolio et al., 2018; Dyson, 2019c; Faeth et al., 2011). I find that these outcomes of development and landscaping activities influence the presence and foraging activity of birds on office developments in Bellevue and Redmond, WA.

### 3.4.1 Vegetation association in urban office developments follows other habitats

The bird species with significant ecological preferences in point biserial correlation analysis support my hypothesis that urban vegetation associations and habitat use is consistent with those observed elsewhere (Poole, 2016). Brown Creeper and Red-breasted Nuthatch are bark foragers reliant on large conifer trees which support their prey species and provide both nesting and wintering habitat. Townsend's Warbler, Golden-crowned Kinglet, and Chestnut-backed Chickadee are canopy foragers primarily in conifer forests. Brown Creepers in particular are a species of concern due to Douglas-fir harvesting, though other species are also under pressure from land use conversion (Poole, 2016). Diets of Red Breasted Nuthatch and Chestnut-backed Chickadee are largely insectivorous but supplement their diets with conifer seeds (Poole, 2016). Only American Crow, a generalist urban species, was associated with the ornamental tree habitat cluster.

Overall, conifer associated native bird species preferred habitat on office developments characterized by native trees, including conifers. The observed bird community on office developments is similar to the bird communities observed in 'young' (40-75 y.o.) and 'mature' (105-165 y.o.) Douglas-fir stands in western Washington (Haveri and Carey, 2000; Manuwal and Huff, 1987). These stand ages correspond with trees planted in the late 1970s following development and preserved Douglas-fir trees that established following logging in the early 1900s.

Demonstrated use and foraging activity provide evidence that office developments provide resources important to individual fitness for winter birds, and is an important first step in establishing habitat quality, habitat selection, and effects on population size (Jones, 2001). My results are consistent with other urban bird research, which found that native bird species were disproportionately associated with native vegetation (Belaire et al., 2014; Burghardt et al., 2009; Chong et al., 2014; Lerman and Warren, 2011; Mackenzie et al., 2014). Additional research quantifying demography (population size, change, and age distribution) and factors influencing habitat selection (e.g. predation, food availability) are needed to definitively assess the habitat quality offered on office developments and their contribution to population size.

### 3.4.2 Variation in bird effective species richness and community composition

I observed very high agreement between univariate regression tests using effective species richness and multivariate tests using community composition. Both analyses identified development and landscaping variables that describe the outcome of developer and land owner decisions to preserve the tree community, resulting land cover, and the resulting tree and shrub community as significant in explaining variation after controlling for the proportion of overcast days. The best model for explaining variation in observed effective species richness and community composition included median dominant Douglas-fir height, after controlling for the proportion of overcast days. This result supports my hypothesis that variables describing the impact of development and landscaping actions on vegetation explain variation in the bird community. However, it does not support my hypothesis that univariate and multivariate analyses would reveal different patterns.

#### Response of feeding guilds

Variation in bird guild effective species richness was variously explained by the three development and landscaping outcomes. Consistent with expectations, conifer associated species were negatively correlated with impervious surface on site and positively correlated with the presence of older, larger trees. This agrees with prior knowledge of birds' habitat preferences and the vegetation preference results of the point-biserial correlation coefficient analysis (Poole, 2016). For example, Red Crossbill is a mature conifer associated species that relies on conifer seeds to overwinter; those I observed belonged to the Pseudotsuga subgroup and were only observed foraging on Douglas-fir cones. Similarly, insectivorous bird effective species richness was negatively correlated with impervious surface on site and positively correlated with the presence of older, larger trees, consistent with other studies (Blair and Johnson, 2008; Zhou and Chu, 2012).

However, omnivorous birds also followed this pattern, which differs from other studies where birds classified as omnivores in other studies are generally urban adapted species (Barth et al., 2015; Chace and Walsh, 2006; Clucas and Marzluff, 2015; Marzluff, 2017). In addition to urban adapted species like American Crow and European Starling, omnivorous species in this study include conifer-associated natives like Red-breasted Nuthatch and Chestnut-backed Chickadee. Red-breasted Nuthatch expands its diet of arboreal arthropods to include large number of conifer seeds (Poole, 2016). Importantly, bird guild assignment varies based on season and location; many species have a more inclusive diet during the winter than during breeding season. For example, Audubon's Warbler is insectivorous during the breeding season, but in the winter expands its diet to include significant amounts of fruit and is thus omnivorous (Poole, 2016). The same bird species therefore requires different winter and summer resources, and winter and summer habitat cues are likely different (Cody, 1985).

### Bottom-up development and landscaping variables are important

Both univariate and multivariate models suggest that "bottom-up" patterns resulting from parcel-level decision making are more important than "top-down" patterns that emerge at the neighborhood-scale from diffuse decisions in determining bird community on office developments (Kinzig et al., 2005) confirming my hypothesis. Site-scale variables including plant selection also explained more variation than neighborhood-scale variables elsewhere in the Pacific Northwest (Galitsky and Lawler, 2015) and on residential properties (Belaire et al., 2014; Daniels and Kirkpatrick, 2006b). These site-scale variables also influence breeding bird diversity and abundance and impact foraging preference (Burghardt et al., 2009; Narango et al., 2017). Differences in insect abundance between native and non-native shrubs are frequently identified as a causal factor (Burghardt and Tallamy, 2013; Burghardt et al., 2009; Tallamy, 2004). These results suggest that for bird habitat use, social-ecological systems are heterogeneous across organizational units in such a way that small scale interactions between social and ecological spheres are more important than more diffuse patterns, at least for highly mobile species like birds.

### Poor support for other bottom-up variables

However, bottom-up socio-economic patterns included in this analysis were not significant in explaining community variation. Most notably, parcel size was not significant here, though area consistently explained biodiversity in residential land uses and parks (Beninde et al., 2015; Evans et al., 2009; Schütz and Schulze, 2015). Since the species-area relationship is well established, different results may be based on different methodological choices or the relative paucity of bird species native to the Seattle area. This study was designed so that there is heterogeneity of vegetation between study units, but each study unit is relatively homogeneous. When area is important, the study unit may be internally heterogeneous, such that additional habitat types and vegetative complexity are included as area increases (Marzluff, 2017; Schütz and Schulze, 2015).

Bottom-up patterns in maintenance inputs were also not significant in explaining measures of bird community. In other studies, irrigation was shown to increases insect prey availability and may increase the diversity of bird communities in arid areas (Schleder, 2010). Here, irrigation is very common, reducing my ability to detect differences; bird foraging in the wet winter months may also be unaffected. More research on the impact of maintenance activities on bird populations and foraging activity is needed in urban areas, as these activities in agricultural areas have long been known to impact bird mortality and foraging success (Fry, 1995; Gibbons et al., 2015; Henny, 1972; Lepczyk et al., 2004; Mineau et al., 1994; Mineau and Tucker, 2002; Mineau and Whiteside, 2013). While pesticide and herbicide use on site did not significantly explain variation in measures of the bird community, there may be a critical exposure issues for sites with older native conifers an high bird foraging use that apply these chemicals. Particularly impacted birds would be ground and shrub foragers and insectivores associated with conifer habitat including Pacific Wren and Varied Thrush, along with sparrows and other wrens. Less impacted would be high conifer foragers if most of their prey (insect or plant) is not exposed.

### Poor support for top-down variables

Top-down neighborhood-scale socio-economic and land cover variables resulting from diffuse decisions made in socio-ecological systems did not receive support in either univariate or multivariate analyses. This result does not support my hypothesis that socio-economic variables significant in other research would be significant here. In studies of residential property, socio-economic neighborhood-scale variables significantly explained variation in bird species richness in studies of residential property (Lerman and Warren, 2011; Luck et al., 2013; Melles et al., 2003). Land cover variables, including surrounding vegetation, tree canopy, and impervious surface cover were also significant (Beumer and Martens, 2015; Heezik et al., 2013; Melles et al., 2003; Schütz and Schulze, 2015). However, there is disagreement in the existing literature, with some studies agreeing with my results that neighborhood-scale variables are less or not important for passerine community composition (Belaire et al., 2014; Daniels and Kirkpatrick, 2006b; Galitsky and Lawler, 2015).

Birds are highly mobile species with ranges that overlap multiple land use types. In Bellevue and Redmond, WA, commercial property is adjacent to residential land use. A bird observed on a commercial parcel also includes residential parcels in its home range. Decisions in social-ecological systems are driven by diverse agents, and decisions on commercial properties are likely driven by different motivations and preferences than residential property. For example, landscaping for self and neighborhood status on residential property versus landscaping to attract tenants on commercial property (Nassauer et al., 2009). The outcome of different decision pathways should theoretically be important to birds only as far as they influence habitat quality. If they impact habitat quality differently, the proportion of different land uses in the area may influence bird communities.

My results suggest that neighboring residential property habitat either doesn't matter, or is of sufficient quality to not affect passerine birds observed on office developments. It may also be that for local species habitat selection processes, the patch of habitat on the office development is more important than what surrounds it. Further behavioral ecology research and studies examining bird use of adjacent land uses is needed.

Methodological differences may partly explain the difference. Most other studies address other land uses, use neighborhoods instead of management units (parcels) as the unit of analysis, or use other bird count methods. My research also did not examine the ends of the socio-economic gradient, while others do not study the entire vegetation gradient. However, these alone can't explain differences in results, my study did agree with some studies on residential land uses using more standard methods (e.g. Belaire et al., 2014). Standardized study designs across multiple urban areas and multiple land use types are needed to determine which factors are important in determining whether site-scale variables, neighborhood-scale variables, or both are significant. Potential explanatory variables include local bird ecology and life history, breeding vs. non-breeding season (as in Clergeau et al., 1998), patterns of development, or some combination of these.

### 3.4.3 Study strengths and limitations

While differences in methodology makes comparison between this research and other studies more difficult, they contributed to the strengths of this study. First, sampling across the vegetation gradient within one land use allowed for detection of significant differences in tree and shrub communities and for detecting patterns of bird habitat association and important parcel-scale variables. These provide the foundation for future policy and management recommendations. Second, using the standardized search method facilitated research in noisy urban areas when birds were not calling, and kept the unit of analysis as the parcel instead of the area of a point count (Watson, 2003). This allowed me to connect parcel-specific management actions with the bird community's habitat use.

There are also important limitations of this study. First, bird studies were conducted during the winter and not year round. Policy and management best practices suggestions made based on winter observations may not capture the stricter summer requirements, and more robust year round research is needed. Second, my site selection did not sample across the full range of surrounding impervious surface and parcel area. This may lead to under-valuing the importance of these variables in models of bird richness and community composition. Finally, habitat use research on its own cannot quantify habitat quality or birds' process of habitat selection without behavioral or life-history information (Jones, 2001; Sherry and Holmes, 1985).

### 3.4.4 Policy and management recommendations

Overall, my results suggest that bird association with a specific office development is best explained by the vegetation community structure and impervious surface cover on that specific parcel. This does not mean that policy implemented at larger scales is not important, instead my results suggest that a critical role of policy is to encourage parcel-scale decision-making and actions that support birds. Where residents are interested in conservation, policy should alter developer and landowner actions to modify the resulting vegetation communities on site to better support local bird species populations.

My recommendations are based on patterns observed in this research on winter bird communities and in studies of breeding birds (Belaire et al., 2014; Kang et al., 2015; Shoffner et al., 2018). Additionally, known bird habitat preference information should be used to manage for habitat used by species of interest (Poole, 2016). For example, if we are interested in native bird species including Brown Creeper and Townsend's Warbler, we should actively promote the native conifer habitat these species are associated with.

One practical implication of bird's relaxed winter foraging requirements is that a wider range of urban properties may be valuable in the winter. Fulfilling winter resource requirements is a crucial part of bird conservation as overwintering survival and body condition influences breeding success (Calvert et al., 2009; Faaborg et al., 2010; Norris et al., 2004; Woodworth et al., 2017).

**Tree retention:** In the Puget Trough, human actions supporting native conifers are important for the continued presence of native forest species including Brown Creeper, Varied Thrush, and Pacific Wren. Established trees provide critical opportunities for foraging, nesting, and perching, and are more beneficial than newly planted replacement trees (Barth et al., 2015; Sung, 2012). Minimizing the loss of conifer trees to the maximum extent practicable is supported both by this work and others (Barth et al., 2015; Shoffner et al., 2018; Shryock et al., 2017; Stagoll et al., 2010). Key exceptions are if a site is extensively infected with a root rot (e.g. *Phellinus sulphurascens*, *Heterobasidion* sp.) or if existing trees are otherwise compromised.

Ideally, city policy would encourage development that avoids "green land" disturbance, and designs that preserve as many trees and as much native soil as possible while also fulfilling client needs.

Other researchers' priorities mirror these; they suggest minimizing forest loss first, then reducing disturbance effects in the matrix (Shoffner et al., 2018). Existing tree protection policies are limited by local politics and developer and landowner compliance, and the efficacy of existing policy is mixed (Hill et al., 2010; Sung, 2012). Other city policies, including parking space requirements and parking lot planting requirements, result in development patterns that favor small cultivated trees over native conifer retention and planting. These policies will need to be changed to better support bird use of sites.

**Planting trees:** Additionally, actions and policies that accomplish long-term urban forest management—particularly planning for succession—will be critical to the future of urban birds in the Puget Trough and elsewhere (Threlfall et al., 2016). In addition to aligning policy to support native tree planting, outreach and initiatives encouraging larger native tree planting may be necessary to overcome the observed bias towards planting smaller ornamental deciduous trees (Tenneson, 2014). While some ornamental non-native trees like seed-bearing *Fraxinus* sp. may selectively provide important food resources, the inclusion of native conifer variables in well supported models and the results of other research studies suggests that native trees are more important (Narango et al., 2017; Schlaepfer et al., 2011). Far more native bird species are associated with the native tree habitat community typology than the ornamental tree habitat community typology, suggesting that planting natives will not negatively impact local bird species, but if these actions are not taken, species could be materially hurt.

While very young trees provide little habitat value (Sung, 2012), trees should become more valuable over time as they mature. For example, older neighborhoods with more mature cultivated vegetation supported higher bird diversity than newly developed neighborhoods (White et al., 2005), and birds prefer foraging in native trees and that these trees support higher prey abundance (Narango et al., 2017). Planting trees also anticipates existing tree death to maintain the future of the urban forest, as planting largely replaces tree dispersion and establishment processes on landscaped properties (Ettinger et al., 2017).

**Planting shrubs:** Planting native shrubs is suggested as a straightforward action to provide food resources to native birds as shrubs are easily planted, grow quickly relative to trees, and provide cover and foraging resources (Cerra and Crain, 2016). Other studies have found that increasing the volume or complexity of understory vegetation increases urban bird species richness (Threlfall et al., 2016). However, landscaping changes on commercial developments (0.5-5 acres) can be expensive; based on anecdotal evidence these changes are outside of the budget for many of the properties in my sample. Additional research on high native shrub richness sites, including post-installation monitoring, is needed specifically in commercial landscapes to evaluate the cost/benefit of shrub community shifts for birds, insects, and other urban wildlife. For example, Varied Thrush often chooses areas with less shrub cover when foraging (Beck and George, 2000).

**Other plantings:** Further, conifer forests are not the only type of habitat historically found in the Puget Trough. Landscaping on office developments imitating grasslands, young forests, or other ecosystems could provide important resources for native bird species and other wildlife while offering design alternatives for developers and landowners when there is no existing forest or retaining trees on site is not feasible. An important question for future research is whether such designs provide resources for desired bird species and other wildlife. Note that this is almost entirely unexplored. During my vegetation classification visits to 400+ properties in Bellevue and Redmond, no property was landscaped in this fashion. Two key limitations likely exist. First, the aesthetics of grasslands are frequently challenging (Hands and Brown, 2002). Second, current policy may preclude these alternative native habitats, necessitating municipalities to grant waivers or alter landscaping codes before they can be tested.

Overall, changing developer and landowner actions and preferences is likely the only way to sustainably alter development patterns, and there are strong arguments for ecologists' involvement in the development process (Felson et al., 2013; Miller and Hobbs, 2002; Niemelä, 1999). In addition to outreach for developers and landowners on the importance of trees both to potential clients (Kaplan, 2007; Lottrup et al., 2012; Nesbitt et al., 2017) and wildlife (this paper; Barth et al., 2015; Shryock et al., 2017; Stagoll et al., 2010), joint research with developers to identify building techniques that are both cost effective and conserve birds are essential. Meaningful sustainability must include a fundamental shift in how sites are developed—moving from a 'tabula rasa' approach where sites are cleared of vegetation and topsoil prior to development to a more place-based and site-specific design and engineering approach.

## 3.5 Conclusion

Parcel-scale development and landscaping actions, including tree removal and planting species selection, directly and indirectly alter vegetation communities and create variation in the vegetation communities on commercial land use (Dyson, 2019c). I found that conifer-associated bird species exhibited clear associations with office developments where native trees were preserved through development and planted during site landscaping. Measures of bird effective species richness and community composition were significantly explained by variables describing the age and density of native conifers, the abundance of native shrubs, and the amount of impervious surface present at the office development. These results provide support for human-mediated changes in vegetation affecting higher trophic levels on office developments in Redmond and Bellevue, WA (Faeth et al., 2011).

My results contribute to our understanding of how human actions at the parcel-scale correlate with bird community composition on commercial land uses, and can help guide policy and management best practices. Evidence that developer and landowner vegetation choices impact bird richness and community composition suggest that actions and policies that accomplish native conifer preservation and the long-term management of the urban forest will be critical to the future of native birds that overwinter in the Puget Trough. These site-scale actions together contribute to the habitat provided by the urban matrix, and increasing habitat quality in the urban matrix contributes to breeding bird success and may reduce the probability of local extinction (Rosenzweig, 2003; Shoffner et al., 2018). There is a significant role for developers, landowners, and policy makers to shape this future. Specific recommendations for the Puget Trough arising from this research include maximizing preservation of existing native canopy cover during development—including designing buildings to preserve trees and soils and avoiding 'green' development—and landscaping with native conifers.

Future research efforts should center on developing building techniques that are both cost effective and foster bird conservation, as changing developer and landowner actions and preferences is critical to sustainably and meaningfully altering development patterns. Where native conifers cannot be preserved or have already been lost, researchers should explore the value to local bird species of planting native conifer and deciduous trees and of alternative native habitats, including grasslands and shrublands mimicking newly disturbed/early successional habitat. Post-installation monitoring to determine the efficacy of suggested approaches is critical, though often ignored, and can also discover unintended consequences including elevated bird-window strike rates (Hager et al., 2017; Hostetler et al., 2011). Finally, birds move across the landscape and have ranges overlapping multiple land use types. More comprehensive research on bird habitat associations and different land uses that relates management units (parcels) to bird presence is needed. More in depth studies of bird behavior and population biology including tracking their movements across cities is needed to better understand how the complex patterns that emerge in social-ecological systems impact bird habitat use.

# Chapter 4

# Development and landscaping actions impacting vegetation explain variation in fungal community composition on office developments

## 4.1 Introduction

Fungal communities in urban ecosystems may be impacted by the outcome of development, landscaping, and maintenance actions taken by diverse human actors including property developers, land owners, landscape architects, and others. These actions alter urban soils and contribute to disturbance and vegetation succession processes, influencing patterns of vegetation community composition and distribution in social-ecological systems (Avolio et al., 2018; Dyson, 2019c; Faeth et al., 2011). In other ecosystems, analogous ecosystem changes have been shown to impact fungal communities and important ecosystem functions provided by fungal communities, including decomposition, nutrient cycling, and plant survival (Van der Heijden et al., 1998; Zak et al., 2003).

Human actions during development include native conifer removal, soil disturbance and compaction, and impervious surface creation. While existing research on urban fungi and changes in fungal community composition driven by human action in social-ecological systems is sparse (Newbound et al., 2012, 2010; Pautasso, 2013), in non-urban settings, fungal community composition is sensitive to changes in the availability of host plants, soil nutrients, and irrigation, though different fungal taxa and trophic groups may respond differently to the same environmental gradient (Batten et al., 2006; Lilleskov et al., 2002; Lothamer et al., 2014; Schimel et al., 2007; Wiklund et al., 1995). Topsoil modifications during development likely destroys the existing fungal community, alters the spore bank present, and alters soil properties. The resulting urban environment and soil conditions are novel and highly heterogeneous, and fungal communities found there provide different ecosystem functions when compared with natural areas (McDonnell et al., 1997; Pouyat et al., 2010).

Landscaping actions change tree and shrub community composition and host species availability (Dorney et al., 1984; Goodness, 2018; Grimm et al., 2017; Heezik et al., 2014; Turner, 2005). Recent research suggests that interactions between ornamental plants and fungi may impact both plant and fungal diversity and community composition, as well as alter properties of urban soils and impact ecosystem function (Batten et al., 2006; Yao et al., 2006). Introducing non-native ornamental plant species alters fungal community composition in other ecosystems. Proposed mechanisms include modifying soil properties including pH and nitrification rates, altering the rhizosphere, and altering leaf litter composition (Ehrenfeld, 2003; Hawkes et al., 2005; Kourtev et al., 2003, 2002; Lothamer et al., 2014; Vivanco and Austin, 2008; Wolfe and Klironomos, 2005; Yao et al., 2006). Additionally, mycorrhizal fungal inoculum is reduced when host plants are removed, suggesting a positive feedback mechanism between mycorrhizal fungi and plant hosts (Vogelsang et al., 2006).

Landscaping actions also augment fungal dispersal processes in social-ecological systems. Some fungal species are imported as non-natives on nursery root stock, including *Paxillus involutus*. Some nurseries and landscaping companies also use fungal inoculants, which may not perform the desired function, may create invasive species problems, and non-sterile inoculum may introduce saprobes and parasites (Schwartz et al., 2006). Products are advertised as effective without species information or consideration for the ecosystem into which they are being introduced. Scientific guidance on detection and removal of non-native fungi is scarce (Dickie et al., 2016).

Maintenance actions including watering, fertilization, mulch addition and litter removal alter nutrient cycling processes and impact fungal community composition (Allison et al., 2007; Gehring et al., 2006; Goodness, 2018; Grimm et al., 2017; Heezik et al., 2014; Jumpponen and Jones, 2010; Lilleskov et al., 2002; Turner, 2005). Irrigation suppresses fruiting in some drought-loving species, and alters mycorrhizal fungal colonization communities (Gehring et al., 2006; Wiklund et al., 1995). Saprotrophic species are less impacted than mycorrhizal species, though wetter microclimates enhance the ability for fungi to colonize substrates (Brantley et al., 2001; Wiklund et al., 1995). Nitrogen addition to systems can result in decreased fungal species richness generally and within particular groups such as ectomycorrhizal fungi, possibly due to loss of competitive advantage in nutrient rich environments (Allison et al., 2007; Avis et al., 2008; Eom et al., 1999; Lehto and Zwiazek, 2011; Lilleskov et al., 2002; Wiklund et al., 1995). Again, saprotrophic species are less impacted than mycorrhizal species by nutrient addition (Wiklund et al., 1995). These changes in fungal community composition may alter decomposition and nutrient cycling ecosystem process (Eom et al., 1999; Lilleskov et al., 2002).

Adding mulch impacts existing fungal communities, stimulating growth and fruiting in species already present in the soil (Bridge and Prior, 2007). Bark, woodchips, and sawdust support different species diversity (Shaw et al., 2004). Mulch formulations that retain water are easier to colonize, while large nuggets are more difficult to colonize as they repel water (Brantley et al., 2001). Mulch is also acidic, and pH is known to influence which species are present (Chalker-Scott, 2007). However, our knowledge about the impacts of adding ornamental mulch on fungal communities is limited (Brantley et al., 2001; Shaw et al., 2004).

Removing dead wood impacts fungal communities; for example, rare and endangered fungal species are generally more abundant with increasing amounts of dead wood (Nordén et al., 2013). In forested systems, fungal species richness has been associated with increased dead tree and downed log recruitment (Dove and Keeton, 2015). Additionally, some research suggests mowing and pruning alter mycorrhizal community composition, while others have found no impact (Barto and Rillig, 2010; Binet et al., 2013; Eom et al., 1999; Gehring and Whitham, 2002; IJdo et al., 2010; Jumpponen and Jones, 2010; Klironomos et al., 2004).

Overall, research in other ecosystems suggest that the outcomes of development, management and landscaping actions may influence fungal community composition in social-ecological systems, with potential impacts on broader ecosystem function and mycorrhizal colonization (Batten et al., 2006; Hawkes et al., 2006). Here, I compare measures of the fungal community observed on office development sites—including effective species richness, community composition, and trophic classification—with variables describing the outcome of human action during development and land management to examine the first part of this chain:

1. What variables describing socio-economic or land cover patterns or variables describing the outcome of development, landscaping, or maintenance actions explain variation in fungal effective species richness?
2. What variables describing socio-economic or land cover patterns or variables describing the outcome of development, landscaping, or maintenance actions explain variation in fungal community composition or trophic group community composition?
3. Is there evidence for fungal community thresholds along the significant environmental gradients identified in Question 2?

I hypothesized that site-scale variables would be more important than neighborhood-scale variables, as there is some evidence that the distribution of fungi across the urban gradient appears more closely related to site-specific soil characteristics stemming from maintenance than landscape-scale variables (Newbound et al., 2012). Also based on previous research, I hypothesized that soil conditions (pH, carbon and nitrogen availability) and sampled ground cover type would be significant in explaining variation in effective species richness and community composition (Jost, 2006; Newbound et al., 2012). Additionally, I hypothesized that measures of effective species richness and community composition would respond differently to environmental gradients like changes in vegetation resulting from development actions, and that ecological gradients would be more important than social gradients. Based on existing trophic information, I hypothesized that variables describing woody debris availability would be significant in explaining variation in fungal species richness and fungal community composition.

I quantified the fungal communities on office development sites using next-generation sequencing (NGS) data from soil samples taken from 17 office development sites and mushroom specimens from 19 office development sites. I quantified soil nutrients, tree and shrub communities, and ground cover proportions, neighborhood- and site-scale socio-economic, neighborhood-scale land cover variables, and variables describing the outcome of development, landscaping, and maintenance actions for each site. I used univariate and multivariate ecology tools to analyze NGS and collected mushroom datasets.

My results suggest that effective species richness is largely uniform across office development sites, while fungal community composition and trophic guild community composition are significantly influenced by development, landscape design and maintenance actions taken by developers and landowners. Actions impacting tree preservation through development, tree and shrub community composition, woody debris availability, and soil chemistry are consistently important, with significant variation explained in PERMANOVA and change points detected in TITAN. However, the relatively small effect size in PERMANOVA suggests a need for further study to verify these results.

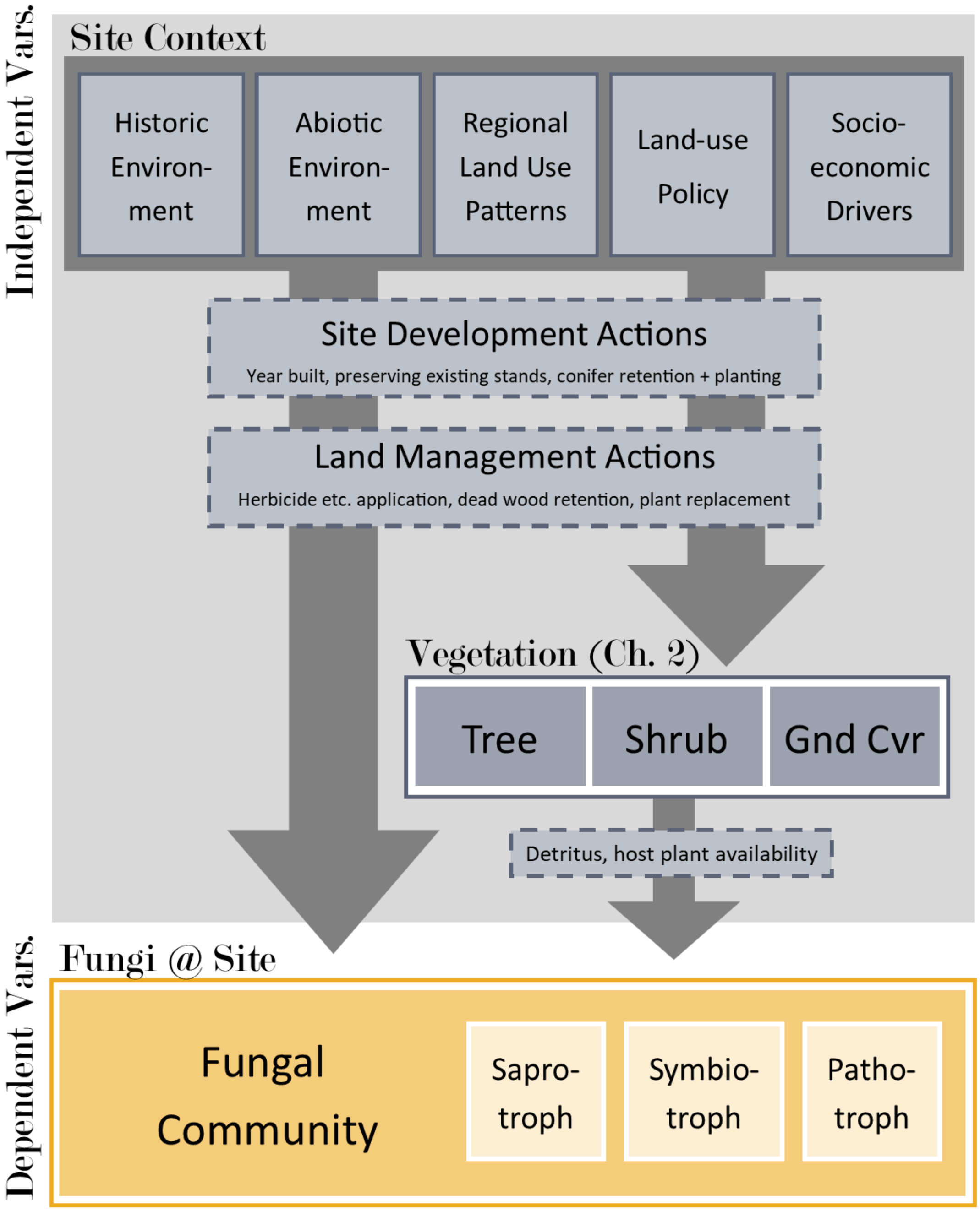

Figure 4.1: An overview of the relationships between measured independent variables and the fungal community present at a site. When a site is developed, the developer's actions determine whether stands of trees and their surrounding soil and root fungal communities are preserved through development, as well as the initial planting design and the year built. These variables are modified by the landscaping and management actions, including plant replacement, herbicide/pesticide/etc. applications, and dead wood removal. These variables may influence fungal community composition.

## 4.2 Materials and Methods

### 4.2.1 Study area

Redmond (2017 population 64,000) and Bellevue (population 144,000) are located east of Seattle in King County, Washington (United States Census Bureau, 2017). Both cities share a similar ecological history, a similar disturbance timeline for logging and agriculture, and have grown considerably since the opening of the Evergreen Point Floating Bridge (SR 520) in 1963 allowed easy access to Seattle. They are at similar elevations ($< 500$ ft) and experience the same climate and weather. The sampling frame was limited to Redmond and Bellevue north of I-90 and excluded developments in Bellevue's central business district.

Study sites were selected using disproportionate stratified random sampling across five vegetation strata to ensure that my sample included sites across the entire vegetation gradient. To avoid confounding factors, I restricted the sampling pool to sites in the 25th to 85th percentile for size and the 15th to 85th percentile for surrounding impervious surfaces (Dyson, 2019c)

I sent three rounds of mailings to the property owner or manager on file in the King County Assessor's database (published October 9th, 2014) requesting access to their property for fungal sampling (King County Department of Assessments, 2014). Of the 46 requests sent, 20 were accepted, 6 were rejected, and 20 received no response or were not deliverable. My final sample included between 3 and 5 sites from each of the five vegetation strata. The study sites ranged from 0.631 acres to 5.39 acres in size. 13 sites were located in Bellevue and 7 of the study sites were located in Redmond. One of the Redmond sites was later excluded due to property access conflicts for a final sample size of 19 sites (Dyson et al., 2018). The office developments on study sites were built between 1975 and 2008. Commercial use of the sites included light industrial, white collar office space, medical/dental offices. Some sites were fully leased to tenants, while others were either partly or fully owner-occupied. Company size ranged from one to many thousand employees.

### 4.2.2 Fungal datasets

I collected two complimentary fungal datasets: a next-generation sequencing (NGS) dataset based on soil samples and a genus dataset based on collected mushroom samples. Community information from the NGS dataset consists of counts of sequence variants (SVs, sometimes called amplicon sequence variants), each representing a unique sequenced gene region (Callahan et al., 2017). Community information for the mushroom samples consists of presence/absence data agglomerated at the genus level for each site.

The two datasets are complimentary. The NGS dataset captures the majority of detectable fungal genetic material present in the soil sample, but cannot distinguish between SVs which are actively part of the ecology on site and SVs which are present only as spores (Peay, 2014). Sampling aboveground mushrooms can only detect fungal species that are actively fruiting and large enough to be seen, which misses those that fail to reproduce, reproduce underground, have extremely cryptic fruiting bodies, or are microscopic. This can bias observed community composition; for example parasitic and endophytic fungi rarely produce mushrooms, and molds and yeasts are microscopic but important saprotrophs (Rodriguez et al., 2009). Strengthening NGS data analysis with physical samples helps to offset the deficiencies of each approach (Hart et al., 2015).

#### Next-generation sequencing dataset

Of the twenty sites in my larger study, 17 agreed to soil sampling, which I completed between November 20 and November 22, 2015. Within each office development, I stratified based on ground cover type as this is known to influence fungal communities and urban ground cover results from and leads to different management regimes (Trinder et al., 2009). Ground cover data was collected in May and June 2015. I sampled three groundcovers: grass, mulch, and areas with groundcover dominated by native tree litter (“unmanaged”). Areas with dense landscaping shrubs, ivy, water, or hard-packed dirt paths were not sampled. Between one and three ground cover types were sampled at each site.

Each sample was a composite sample comprising five randomly placed subsamples. Ten survey points were generated for each ground cover type (ESRI, 2011); points 1-5 were the target sample points with 6-10 used in order as replacement points in case field conditions precluded sampling at one of the first five points. The presence of soil where the probe could not be inserted to a 5 cm depth is common in heavily modified urban soils. Soil samples were extracted from the 0-5 cm layer with an 401.03 Soil Recovery Probe after removing the surface layer of mulch, litter, or grass. Between samples, but not subsamples, the probe was cleaned using a nylon test tube brush and denatured alcohol. All soil samples for an individual site were placed in a cooler with dry ice at the conclusion of sampling for that site. At the conclusion of fieldwork, soil samples were homogenized and wet sieved before being held at University of Washington in a -20 °C freezer until January when they were shipped overnight with dry ice to the Fierer Lab at University of Colorado at Boulder (Hart et al., 2015).

The Fierer lab extracted DNA from each soil sample using the MoBio PowerSoil DNA isolation kit (MoBio Laboratories, Inc., Carlsbad, CA, USA). Using ITS1-F/ITS2 barcoded primers, the first internal transcribed spacer (ITS1) region of the rRNA operon was amplified in triplicate and sequenced (Crowther et al., 2014). The lab used the PicoGreen DNA assay to quantify PCR products from all samples before pooling them in equimolar concentrations. The UltraClean PCR Clean-up Kit was used to clean and concentrate amplicons (MoBio Laboratories, Inc., Carlsbad, CA, USA). An Illumina MiSeq instrument using the paired-end v2 300 cycle MiSeq kit was used to sequence the samples at the University of Colorado Next Generation Sequencing Facility (Barberán et al., 2015; Crowther et al., 2014; Rojas et al., 2016). I used only the forward reads for this analysis due to quality issues in the reverse reads. I demultiplexed the forward-read sequences using a Python script written by the Fierer lab (Leff, 2017) and used the reverse-complimented ITS1-F and ITS2 sequences and the BBDuk Java script from the BBMap package to remove any barcoded primers from the demultiplexed sequences (Bushnell, 2017).

I trimmed the first 10 base pairs of each read based on FastQC analysis (Babraham Bioinformatics, 2016) and filtered the forward reads using dada2 (Callahan et al., 2016). Dereplicated reads were assigned to sequence variants (SVs) based on error rates learned from the dataset, then used to construct a table with sequence counts for each sample. dada2's approach using modeled error rates allows the creation of SVs at very high resolution (to single nucleotide differences). Traditional methods use clustering of sequencing reads at ~97% similarity to produce operational taxonomic units (OTUs). Both the increased resolution and the inherent biological meaning of sequence variants make dada2 and SV pipelines a more advantageous choice than OTU pipelines (Callahan et al., 2016). After removing chimeras, the sequence variants were compared with the January 2017 UNITE database using a native implementation of the RDP's naïve Bayesian classifier to assign taxonomic identification (Callahan et al., 2016; Kõljalg et al., 2013; Wang et al., 2007).

Analyses were performed with SVs as the biological unit of analysis. Aggregation to genus is unreliable as UNITE matches may be missing or incorrect (Kõljalg et al., 2013). Aggregation can fail to combine sequence variants without matching UNITE taxonomic information, resulting either in a dataset with mixed aggregation levels or the loss of significant portions of the dataset to achieve uniform aggregation. I removed very rare sequence variants (global $n \leq 10$) from my dataset. For NGS derived datasets, rare sequences may include PCR and sequencing artifacts or true species detections. However, unless a study is determining precise biodiversity estimates, discarding rare sequences is unlikely to alter the results of downstream community analysis (Brown et al., 2015).

Other statistical difficulties inherent to NGS datasets like over dispersion and heteroscedasticity cannot be addressed with rarefaction (Hart et al., 2015; McMurdie and Holmes, 2014). Instead, I used the square root transformation to downweigh the importance of the most abundant SVs (Nguyen et al., 2014). For univariate analysis, I calculated effective number of species (effective species richness; defined as exp(Shannon entropy); see Jost, 2006) for each sample as the response variable.

### Fungal fruiting body data collection

I collected fungal fruiting bodies (mushrooms) from 19 of the 20 sites in the larger study. The remaining site was sampled once before staff turnover restricted access (Dyson et al., 2018). I conducted site visits between 28 September and 25 November, 2015. In the Puget Sound, many fungal species fruit in the wet fall months, and the first freeze destroys most soft-bodied mushrooms (Ammirati, personal communication; Halme et al., 2012).

Each site was sampled multiple times to accommodate species-specific differences in timing of fruiting and increase species group detectability (Halme et al., 2012; Lodge et al., 2004). All 19 sites were visited 2-3 times at approximately 3 week intervals throughout the sampling season (Halme et al., 2012). On each site visit, I carried out a complete site macrofungi census. I methodically searched all accessible pervious surfaces, including all planting beds and lawns, under trees, and on and around deadwood. I photographed each mushroom in situ, assigned it a unique ID, and documented the location where it was found. Mushrooms in poor condition (rotten, waterlogged, or dead) were not collected, but were photographed and given a unique ID.

Fungal samples were stored at 0-5 °C, then identified to genus or species by Dr. Joseph Ammirati and preserved via dehydration for future study. At completion of the study, samples will be housed at the University of Washington Herbarium with the exception of four samples identified as *Mycetinis scorodonius f. diminutivus* housed at the University of Tennessee (Petersen and Hughes, 2017).

Analyses were performed with aggregated genus as the unit of analysis. Unlike the NGS dataset where sequence variants have biological meaning and are separated based on genetic differences, the identification to species of physical samples relies on high quality collected samples. Since it is not possible to determine the number of distinct organisms of each fungal species present at each site, collections data is presence/absence data. I did not use any rare species filtering for my collections based dataset, and no further transformations were applied prior to multivariate analysis.

### Assigning trophic classifications

I used FUNGuild to add fungal guild information to the NGS taxonomic information (Nguyen et al., 2016). As not all genera found in my both datasets are represented in FUNGuild, Dr. Ammirati and myself used accepted reference texts and other scientific databases to fill in the missing trophic information. While the saprotroph/symbiotroph/pathotroph grouping is often used, many fungal taxa belong to multiple trophic guilds (Brundrett, 1991; Lindahl and Tunlid, 2015; Lindahl et al., 2002; Shah et al., 2016).

Saprotrophic fungi use a diverse set of enzymatic pathways to decompose wood and litter; saprotrophs are often grouped into white rot, brown rot, and soft rot groups based on which compounds are readily degraded (Riley et al., 2014; Wal et al., 2013). White rot fungi more frequently decompose hardwoods than conifers, while brown rot fungi leave lignin intact and primarily decompose conifers (Floudas et al., 2012; Martínez et al., 2010). These processes recycles complex organic matter and also contributes to degradation of human infrastructure (Blanchette, 2000; Isaacs et al., 2016; Martínez et al., 2010; Rabinovich et al., 2004). The rate of decomposition varies based on litter or wood quality, composition of the decomposer community, and the physiochemical environment (Hättenschwiler et al., 2005; Krishna and Mohan, 2017; Wal et al., 2015). Leaf litter and coarse woody debris provide different environments for decomposition and are exploited by different communities. Leaf litter itself varies significantly; litter may be rich or poor in easily available carbon and nutrients, and may contain additional compounds such as tannins which inhibit decomposers (Gessner et al., 2010; Ivarson and Sowden, 1959). Coarse woody debris is comparatively carbon rich and nutrient poor (including N, P, K; Laiho and Prescott, 2004). Interestingly, white- and brown-rot fungi differentially influence soil acidity, which in turn contributes to determining what species of mycorrhizal species are present (Ammirati, personal communication, Vane et al., 2005).

Symbiotrophic fungi, including mycorrhizal fungi and the lesser understood endophytic fungi, form partnerships with plant species, enhancing mineral nutrient and water acquisition by plant species and influencing plant community composition (Brundrett, 1991; Jeffries et al., 2003; Lehto and Zwiazek, 2011). Different groups of mycorrhizal fungi interface with, influence plant uptake of water, and transfer different soil nutrients to their host plant in different ways (particularly Phosphorous; Jeffries et al., 2003; Lehto and Zwiazek, 2011; Reynolds et al., 2005; Van Der Heijden et al., 2017). As a result, community composition of mycorrhizal fungi plays an important role in plant growth and resistance to drought, competition, and disease (Bennett et al., 2006; Groot et al., 2002; Hoeksema et al., 2010; Jung et al., 2012; Lehto and Zwiazek, 2011; Newsham et al., 1995; Pozo and Azcón-Aguilar, 2007; Swift et al., 1979). As a result, mycorrhizal fungi are a major factor influencing plant biodiversity, community composition and attendant ecosystem functions (Brundrett, 1991; Dahlberg, 2001; Francis and Read, 1994; Hoeksema et al., 2010; Newsham et al., 1995; Read et al., 2004; Van der Heijden et al., 1998; Van Der Heijden et al., 2003; Van Der Heijden and Scheublin, 2007). By supporting trees and other plants, mycorrhizae also contribute indirectly to other ecosystem functions including gas regulation, climate regulation, disturbance prevention, water regulation, soil retention, nutrient regulation, and habitat provision (Groot et al., 2002; Read et al., 2004).

Pathotrophic fungi are dependent on a host organism (plant, animal, fungi, bacteria, algae) for resources. In urban areas pathotrophs infect landscaping plants, urban trees, and (more rarely) humans (Mendgen et al., 1996; Moore, 1959). Urban trees may be more susceptible to parasitic fungi due to frequent pruning (Schubert et al., 2008). Parasites modify food webs and trophic interactions, competition between organisms, and energy and nutrient transfer (Lafferty et al., 2006; Preston and Johnson, 2010). For example, fungal parasites impact the primary productivity of their plant hosts, exerting significant top-down control on biomass (Mitchell, 2003).

### 4.2.3 Independent Variables

#### Detection variables

For the collection dataset, the number of visits per site, proportion of ground covers, and recent weather could impact detection. I calculated total rainfall over the week prior to each sampling event and the median average daily temperature over the 7 days prior to site visitation (AgWeatgerNet Team, Washington State University, 2016). Weather was not compared between sites per se but rather between the site's sampling events in order to determine if the recent weather conditions when sampling occurred might account for differences in observed mushroom communities.

#### Soil variables

Soil from each sample was dried, homogenized, and sieved on clean equipment prior to testing at the University of Washington School of Environmental and Forest Sciences Analytical Services lab. Total Carbon, Nitrogen, and Hydrogen concentrations were measured using dry combustion (Method 29-2.2, Nelson and Sommers in Page et al. 1982) with a 2400 series CHNS/O elemental analyzer. pH was measured using a HM Digital model PH-80 pH meter; a standard weight of soil was mixed with water and the pH of this solution was measured following proper standardization with a solution of known pH (Method 12-2; McLean, 1982).

For the collections dataset, average soil values (pH, C, N) were calculated based on the stratified ground cover samples. Area-based weighting was used for carbon, and nitrogen concentrations ($\frac{\sum(\text{GC area x value})}{\sum(\text{all GC areas})}$). pH values were first converted to H+ concentration, area-based weighted average calculated, then converted back to pH values ($-log_{10}\frac{\sum(\text{GC area x H+ concentration})}{\sum(\text{all GC areas})}$).

### Vegetation data

**Tree Community:** At each site, individual trees > 4" DBH were identified to genus or species where possible (Dirr, 2009, 1997; Schoon, 2011; Sibley and others, 2009; Symonds, 1958). Flexible beta clustering and indicator species analysis were used to identify two predominant tree community typologies, characterized by native and ornamental species. I also derived other tree stand variables, including Douglas-fir height as a proxy for tree age, stands predating development via historical records, and native conifer density (Dyson, 2019c).

**Shrub Community:** At each site, all members of the shrub community were identified to genus or species (Brenzel, 1995, 1995; Dirr, 2009, 1997; Symonds, 1963). I used flexible beta clustering and indicator species analysis to identify two shrub community typologies, characterized by native and ornamental species. I derived other variables from the shrub community including the density of native shrubs and effective species richness of native shrub species (Dyson, 2019c; Jost, 2006; U.S. Geological Survey, 1999; USDA, 2016).

Table 4.1: Definitions of independent variables used in fungal analyses.

| Variable Name | Definition | Data Source |
|---|---|---|
| **1.** | **DETECTION VARIABLES** | |
| **Ground Cover Type (NGS)** | Ground cover type sampled (grass, mulch, unmanaged). | Site survey |
| **Number of Visits per Site (Collections)** | The number of site visits in fall 2015. | Site survey |
| **Detectible Ground Cover Proportion (Collections)** | Proportion of pervious area that has high detectability of mushrooms (grass, mulch). | Site survey |
| **Median Average Air Temperature (F, Collections)** | Median of prior average 7-day air temperature (F) for all mushroom collection visits. | WSU AgWeatherNet |

| | | |
|---|---|---|
| **Median Average Soil Temperature at 8in (F, Collections)** | Median of prior average 7-day soil temperature (F) at 8 inches depth for all mushroom collection visits. | WSU AgWeatherNet |
| **Median Total Precipitation (inches; Collections)** | Median of prior 7-day total amount of precipitation in inches for all mushroom collection visits. | WSU AgWeatherNet |
| **2.** | **VEGETATION GROUPS** | |
| **Tree Community Typology** | Broad tree community (native or ornamental) based on flexible beta cluster analysis of tree density data. | Site survey |
| **Shrub Community Typology** | Broad shrub community (native or ornamental) based on flexible beta cluster analysis of shrub density data. | Site survey |
| **3.** | **SITE-SCALE SOCIO-ECONOMIC VARIABLES** | |
| **Area (acre)** | Site area, in acres. | King County Assessor |
| **Town** | Location, Bellevue or Redmond. | King County Assessor |
| **Building Age (in 2017)** | Age of building on site (or mean age for multiple buildings) in 2017. | King County Assessor |
| **Building Quality** | Categorical 'quality class' assigned to buildings on the parcel. | King County Assessor |
| **Appraised Land Value per Acre** | Appraised land value divided by site area. One missing assessed land values were replaced with population median land value. | King County Assessor |
| **4.** | **NEIGHBORHOOD-SCALE LAND COVER AND SOCIO-ECONOMIC VARIABLES** | |
| **Impervious w/in 500 m (%)** | Percent of impervious surface within 500 m of the site's perimeter. | National Land Cover Database 2011 Percent Developed Imperviousness dataset updated in 2014 |
| **Tall Vegetation w/in 500 m (%)** | Percent of tall tree vegetation canopy cover within 500 m of the site's perimeter. | NDVI calculated using the 2015 NAIP data and object height calculated using 2014 and 2013 LiDAR data |
| **Short and Medium Vegetation w/in 500 m (%)** | Percent of short and medium vegetation canopy cover within 500 m of the site's perimeter. | NDVI calculated using the 2015 NAIP data and object height calculated using 2014 and 2016 LiDAR data |
| **Major Intersections w/in 500 m (count)** | Number of major intersections located within 500 m of the site's perimeter. | OpenStreetMap |
| **Median Income** | The median income of residents for the site's block group. | American Community Survey 2014 5-year block group |

| | | |
|---|---|---|
| **Percent Foreign-Born** | The percent of residents born outside of the United States for the site's block group. | American Community Survey 2014 5-year block group |
| **5.** | **SOIL VARIABLES** | |
| **pH** | Average pH area-weighted by ground cover strata area. | Soil sampling |
| **C:N** | Ratio of Carbon to Nitrogen of sites, area-weighted by ground cover strata area. | Soil sampling |
| **Nitrogen, Carbon concentrations (%)** | Average C or N concentration area-weighted by ground cover strata area. | Soil sampling |
| **6.** | **DEVELOPMENT, LANDSCAPE, AND MAINTENANCE VARIABLES** | |
| **Impervious on Site (%)** | Percent of the parcel's area occupied by impervious surface. (Development) | Site survey |
| **Stands Predate Development** | Indicates presence of a stand of three+ trees nearby one another that predate development. (Development) | Site survey |
| **Median Height of Dominant Douglas-fir** | Median height (m) of 5 dominant Douglas-fir, as a proxy for age. (Development) | Site survey |
| **Density of Native Conifers** | Total density of Douglas-fir, western red cedar, and western hemlock. (Development/ Landscape) | Site survey |
| **Native Shrub Effective Species Richness** | Effective species richness is calculated as exp(H'), following @jost2006. (Landscaping) | Site survey |
| **Density of Native Shrubs** | Combined density of all native shrub species (# / site area in acres). (Landscaping) | Site survey |
| **Cleanup** | Indicates whether the landscaping crew removes detritus from the site. (Maintenance) | Interviews and site survey |
| **Irrigation** | Indicates whether irrigation is used during the summer months. (Maintenance) | Interviews and site survey |
| **Mulch, Herbicide, and/or Fertilizer Application** | Variables (3) indicating whether landscaping crew applies mulch, herbicides, or fertilizers to a site. (Maintenance) | Interviews and site survey |
| **Mushroom Weeding** | Indicates whether the landscaping crew removes above-ground mushrooms. (Maintenance) | Interviews and site survey |
| **Dead Wood** | Total abundance of stumps, logs, and snags on site. (Maintenance) | Site survey |

### Maintenance data

I interviewed landscaping services for the office developments using the elite interview technique and supplemented these interviews with observational data from site visits (Dexter, 1970; Harvey, 2011). I then assigned a value (Yes, No, Unknown) to variables based on performance of the following maintenance activities at each site. I removed “Insecticide” and “Fungicide” application from further consideration as there were no “Yes” responses.

I also censused each site for logs, snags and stumps. Logs were more than 6” in diameter; snags were more than 6” in diameter and more than 2 m tall, stumps were less than 2 m tall. Shrub stumps were not counted towards the total. Multi-trunk stumps were counted only once. Stumps where the tree had grown from a co-dominant trunk were counted.

### Parcel- and neighborhood-scale socio-economic and land cover variables

I derived parcel- and neighborhood-scale socio-economic variables from existing databases (Homer et al., 2015; King County Department of Assessments, 2014; King County GIS Center, 2014; OpenStreetMap Foundation, 2017; QGIS Development Team, 2016; United States Census Bureau, 2016; Xian et al., 2011). Decisions on commercial properties are likely driven by different motivations and preferences than residential properties. However, I included demographic variables to determine if patterns found in residential property are also applicable to commercial property or if characteristics of the surrounding residential property impacted office developments. Other parcel-scale variables are rooted in commercial property valuation including building quality and assessed land value.

To calculate vegetation cover measures, I first calculated NDVI from the 2015 NAIP data (USGS, 2015). I also calculated object height from 2014 Redmond LiDAR data and 2016 King County LiDAR data by subtracting the digital terrain model from the digital surface model (Quantum Spatial, 2017, 2014). I classified pixels as tall tree canopy when $\text{NDVI} \geq 0.15$ and object height $\geq$ 50 feet and as short and medium height vegetation when $\text{NDVI} \geq 0.15$ and object height $<$ 50 feet (Dyson, 2019c).

### 4.2.4 Data Analysis

Data analysis methods are summarized in Figure 4.2.

#### Explaining variation in effective species richness

I used effective species richness calculated as the exponent of Shannon entropy (Jost, 2006). For the NGS dataset where there was more than one ground cover sample per site, I calculated the Euclidian average of effective species richness. I tested each independent variable in a simple univariate model using a custom wrapper for the adonis2 {vegan} PERMANOVA implementation with the Euclidian distance matrix to partition variation (Bakker et al., 2012; Dyson, 2018; Oksanen et al., 2017). Significance was assessed on pseudo-$F$ $p$-values at $\alpha \leq 0.05$. For significant variables, I calculated AICc for single, two, and three variable models using a custom function based on Residual Sums of Squares.

#### Explaining variation in fungal community structure

For both datasets, I used PERMANOVA to identify variables that explain variation in fungal or trophic community composition and NMDS for visualization (metaMDS; Oksanen et al., 2017). For the split-plot NGS dataset, I tested for the influence of ground cover using y ~ site + ground cover. To test other variables, I first used principal coordinates analysis (PCoA) to express the location of Bray-Curtis distances for the 34 site-ground cover samples in Euclidian space, then calculated centroids for each of the 17 sites (Oksanen et al., 2017). The Euclidian distances between centroids was used in further PERMANOVA analysis (Anderson, 2001, Oksanen et al. (2017)). I used the same PERMANOVA testing procedure for multivariate analysis as in univariate analysis. I also used ANOVA to test for significant differences in categorical group dispersion using anova(betadisper()) {stats} {vegan} (Oksanen et al., 2017).

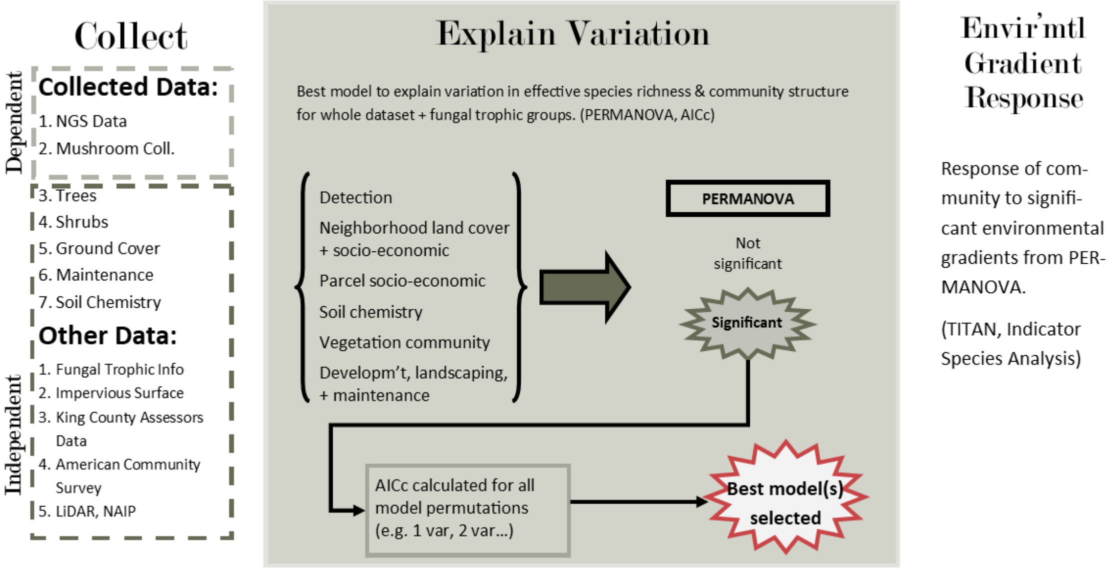

Figure 4.2: Summary of data analysis methods for fungal communities.

### Community response to environmental gradients

I examined habitat associations for sampled ground cover types (NGS data only) and community change along an ecological gradient for independent variables with significant pseudo-$F$ values in PERMANOVA.

Correlation indices are “used for determining the ecological preferences of species among a set of alternative site groups or site group combinations” (De Cáceres, 2013b). I used both Pearson’s phi coefficient of association, which measures the correlation between two binary vectors (for collections presence matrix) and its abundance-based counterpart the point biserial correlation coefficient (for NGS abundance matrix) via the multipatt {indicspecies} function (De Caceres and Legendre, 2009; De Cáceres et al., 2010). I used a custom wrapper to run the function 100 times and kept only indicator species present in $> 50\%$ of the runs. I kept those with a mean index value $> 0.5$.

TITAN uses binary partitioning by indicator value (building on the IndVal function in De Caceres and Legendre, 2009) and is a “method for detecting and interpreting individual taxa contributions to patterns of community change along novel environmental gradients” (Baker and King, 2013). TITAN distinguishes taxa that negatively (z-) or positively (z+) respond to the gradient (Baker and

King, 2010). Taxa are evaluated on their purity (consistent direction of response), their reliability (consistent magnitude of response), and whether a narrow range exists for change-point estimation (Baker and King, 2013, 2010). Bootstrap replicates are used to estimate the width of change-point estimation; taxa with sharp, nonlinear responses have narrow intervals, while taxa with gradual responses will have wider intervals. Synchronous change in many taxa at a given gradient value can be interpreted as evidence for a community threshold, while asynchronous change in taxa may indicate linear or random response dynamics (Baker and King, 2010). I assessed community change using the titan {TITAN2} R implementation of Threshold Indicator Taxa Analysis (TITAN; Baker et al., 2015). The purity threshold was set to 0.95 and the reliability to 0.90 for NGS data and 0.75 for collections data, and I used 250 permutation and 500 bootstrap replicates respectively.

## 4.3 Results

### 4.3.1 Fungal observations

Next generation sequencing identified a total of 1571695 reads across all 34 samples (range: 32960 to 65215 per sample, mean = 46226.3 ± 7316.2). Of these raw reads, 87.8% passed filtering and denoising steps and 87.403% passed chimera detection.

The UNITE database identified 19966 sequence variants, of which 8939 sequence variants belonged to the kingdom Fungi and were observed more than 10 times globally (44.8%). The total number of sequence variants identified to genus or species were 1725 and 2743 respectively. 1972 SVs could only be identified only to kingdom. Sequence variant effective richness of each sample ranged from 40.931 to 192.16 SVs.

We collected and identified 138 unique genera of fungi in 2357 collected mushroom samples from 19 sites. Of these, 38 genera were found only on one site and 1 genus was found on all 19 sites (median = 3 sites, mean = 4.6 sites ± 4.1 sites). The most commonly observed genera were Mycena (19 sites), Inocybe (18), Amanita (15), Gymnopus (15), Psathyrella (15), and Rickenella (14). Genus effective richness at each site ranged from 8 to 47 genera (median = 24, mean = 28.1 ± 12.1).

We identified a new forma in the collections dataset, *Mycetinis scorodonius* f. *diminutivus*. This forma is characterized by diminutive basidiomata, possibly due to the paucity of the substrate on which it is found and other urban stress. All four known samples were found in mulched planters at two of the office developments in this study (Petersen and Hughes, 2017). Additional forma and species may be discovered in urban areas with careful collection.

### 4.3.2 Taxonomic comparison between datasets

On the 17 sites sampled using both methods, 70 genera were found with both data collection methods. Unique genera were detected both in the collections (64 genera) and NGS datasets (495 genera; see Appendix C: Fungi). Two unique genera were found on the sites where mushrooms but no soil samples were collected: Gyroporus and Resinomycena. Parasitic fungi were not well represented; they were detected on only 15 of 19 mushroom sampling sites and the number of SV reads for pathotrophic fungi is approximately 1/3 that of saprotrophic fungi.

### 4.3.3 Independent variables

Weather in October of 2015 was warmer and drier than historical records, while November was significantly cooler and wetter than historical records (2009-2018; AgWeatgerNet Team, Washington State University, 2016). Precipitation follows a bimodal distribution, likely because mushroom sampling occurred outside of stormy periods (either very little in the past 7 days or multiple inches following a storm). Urban soils are heterogenic and exhibit variation in all measures of soil nutrients. Soils in this study were all acidic, with fairly low carbon to nitrogen ratio (C:N) with the exception of mulched ground cover. See Appendix C for additional detail.

### 4.3.4 Explaining variation in effective species richness

For the NGS dataset, only C:N was significant (unadjusted $p$-value NA, variation explained: 33.721%). Increasing C:N was negatively correlated with effective sequence variant richness (Spearman's = -0.27).

For the collections dataset, the number of visits was a significant detection variable (unadjusted *p*-value 0.016, variation explained 0.305%). After controlling for the number of visits, dead wood count, the % impervious surface on site, and the assessed land value per acre were significant. The two best supported models included the number of visits, assessed land value/acre, and either dead wood count or % impervious surface on site (see tables in Appendix C). These models explained 77.63% of variance. Individual Spearman's correlations with effective species richness were negative for increasing % impervious and assessed land value/acre (Spearman's = -0.417 and -0.32 respectively), and positive for increasing number of visits and dead wood abundance (Spearman's = 0.569 and 0.305 respectively).

### 4.3.5 Explaining variation in fungal community composition

Ground cover type significantly explained variation in community composition based on the NGS dataset, however tests of dispersion suggest that differences in spread, not location, are responsible (Table 4.3). The 'unmanaged' ground cover type exhibited the biggest difference in location and in dispersion, which may be a function of small sample size.

Weighted averages of pH and C:N were significant for all NGS analyses, including saprobic, symbiotic, and parasitic trophic sub-groups. The presence of stands predating development and native shrub effective species richness were also significant variables for all NGS analyses. Tree community group (native vs. ornamental tree communities) explained variation in all sub-groups but the symbiotic community. No variables describing socio-economic gradients were significant.

There were no clear best models explaining variation in community composition. For all fungal community groups, all single variable models received equal support along with many two variable models (variation explained: 8-16%; Appendix C: Fungi).

For the collections dataset, as with the NGS dataset, weighted average C:N was significant in explaining overall and saprobic community composition and weighted average % nitrogen for all collected fungal communities. Note that soil variables cannot be directly compared with other variables as soil data was collected on only 17 sites.

As with the NGS dataset, variables describing development and landscaping actions were significant in explaining variation in total fungal community and one or more of the trophic sub-groups

Multivariate PERMANOVA Results (unadjusted p-val)

| | Detection Variables | | | | | Soil Variables | | | | Vegetation Groups | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Detectible Ground Cover % | Median Average Soil Temp @ 8in | Median Total Precip | Median Average Air Temp | Visits/Site | Weighted pH | Weighted C:N | Weighted %C | Weighted %N | Vegetation Class | Tree Community Group | Shrub Community Group |
| Next-Generation Sequencing Data | | | | | | | | | | | | |
| All Sequence Variants | | | | | | 0.0006 | 0.287 | 0.023 | 0.256 | 0.032 | 0.041 | 0.193 |
| Saprobic Sequence Variants | | | | | | 0.006 | 0.042 | 0.140 | 0.272 | 0.053 | 0.026 | 0.133 |
| Symbiotic Sequence Variants | | | | | | 0.009 | 0.045 | 0.076 | 0.250 | 0.094 | 0.066 | 0.400 |
| Parasitic Sequence Variants | | | | | | 0.001 | 0.030 | 0.122 | 0.223 | 0.052 | 0.035 | 0.266 |
| Mushroom Collection Data | | | | | | | | | | | | |
| All Mushrooms | 0.476 | 0.191 | 0.422 | 0.110 | 0.115 | 0.667 | 0.037 | 0.276 | 0.021 | 0.559 | 0.004 | 0.382 |
| Saprobic Mushrooms | 0.747 | 0.230 | 0.498 | 0.132 | 0.072 | 0.945 | 0.008 | 0.551 | 0.024 | 0.276 | 0.00004 | 0.163 |
| Symbiotic Mushrooms | 0.216 | 0.089 | 0.715 | 0.083 | 0.484 | 0.466 | 0.372 | 0.126 | 0.034 | 0.891 | 0.707 | 0.803 |
| Parasitic Mushrooms*[2] | 0.256 | 0.086 | 0.238 | 0.032 | 0.052 | 0.243 | 0.624 | 0.017 | 0.014 | 0.418 | 0.047 | 0.093 |

| | Socio-economic Variables | | | | | | | | | | | GCT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Site Area (acres) | Building Age | Building Quality | Impervious % w/in 500m | Intersections w/in 500 m | Town | Assessed Land Value per Acre | Median Income | % Foreign-Born | Short/Med Veg Cover w/in 500 m | Tall Tree Cover w/in 500 m | Ground Cover Type |
| Next-Generation Sequencing Data | | | | | | | | | | | | |
| All Sequence Variants | 0.856 | 0.209 | 0.333[1] | 0.322 | 0.401 | 0.767 | 0.112 | 0.804 | 0.238 | 0.483 | 0.290 | 0.031[1] |
| Saprobic Sequence Variants | 0.839 | 0.229 | 0.404[1] | 0.440 | 0.468 | 0.607 | 0.137 | 0.810 | 0.282 | 0.491 | 0.363 | 0.043[1] |
| Symbiotic Sequence Variants | 0.895 | 0.209 | 0.550[1] | 0.361 | 0.401 | 0.947 | 0.042 | 0.807 | 0.352 | 0.432 | 0.276 | 0.151[1] |
| Parasitic Sequence Variants | 0.802 | 0.228 | 0.295[1] | 0.257 | 0.487 | 0.652 | 0.208 | 0.619 | 0.391 | 0.374 | 0.315 | 0.016[1] |
| Mushroom Collection Data | | | | | | | | | | | | |
| All Mushrooms | 0.044 | 0.438 | 0.299 | 0.599 | 0.573 | 0.320[1] | 0.124 | 0.201 | 0.620 | 0.192 | 0.528 | |
| Saprobic Mushrooms | 0.027 | 0.612 | 0.064 | 0.610 | 0.487 | 0.116[1] | 0.076 | 0.094 | 0.820 | 0.101 | 0.427 | |
| Symbiotic Mushrooms | 0.623 | 0.281 | 0.870 | 0.656 | 0.859 | 0.730 | 0.406 | 0.935 | 0.602 | 0.517 | 0.664 | |
| Parasitic Mushrooms* | 0.326 | 0.841 | 0.529 | 0.436 | 0.112 | 0.232 | 0.327 | 0.502 | 0.213 | 0.099 | 0.103 | |

| | Development + Land Management Variables | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Irrigation | Mulching | Herbicide Application | Fertilizer Application | Mushroom Weeding | Dead Wood | % Impervious on Site | Stands Predate Development | Median Doug-fir Height (m) | Native Conifers Density | Native Shrub Density | Native Shrub Eff. Sp. Richness |
| Next-Generation Sequencing Data | | | | | | | | | | | | |
| All Sequence Variants | 0.351 | 0.792 | 0.178 | 0.797 | 0.673 | 0.243 | 0.543 | 0.007 | 0.301 | 0.327 | 0.327 | 0.026 |
| Saprobic Sequence Variants | 0.343[1] | 0.758[1] | 0.157[1] | 0.812[1] | 0.727 | 0.259 | 0.451 | 0.010 | 0.262 | 0.476 | 0.330 | 0.035 |
| Symbiotic Sequence Variants | 0.389[1] | 0.785[1] | 0.255 | 0.751[1] | 0.717 | 0.240 | 0.383 | 0.003 | 0.223 | 0.524 | 0.248 | 0.032 |
| Parasitic Sequence Variants | 0.345[1] | 0.755[1] | 0.256 | 0.859[1] | 0.554 | 0.259 | 0.743 | 0.012 | 0.416 | 0.873 | 0.605 | 0.024 |
| Mushroom Collection Data | | | | | | | | | | | | |
| All Mushrooms | 0.016[1] | 0.022 | 0.392 | 0.263 | 0.456 | 0.122 | 0.002 | 0.014 | 0.156 | 0.001 | 0.379 | 0.050 |
| Saprobic Mushrooms | 0.107[1] | 0.022[1] | 0.305 | 0.514 | 0.338 | 0.076 | 0.004 | 0.007 | 0.131 | 0.0002 | 0.328 | 0.051 |
| Symbiotic Mushrooms | 0.014[1] | 0.272 | 0.357 | 0.203 | 0.670 | 0.256 | 0.152 | 0.098 | 0.554 | 0.425 | 0.528 | 0.061 |
| Parasitic Mushrooms* | 0.149[1] | 0.127[1] | 0.521 | 0.055 | 0.144 | 0.491 | 0.0003 | 0.130 | 0.011 | 0.016 | 0.044 | 0.002 |

* : Uses a subset of sites; 17 of 19

[1] : Significant difference in dispersion

[2] : Air temp used as control variable

Figure 4.3: Summary of all PERMANOVA results for both NGS and mushroom collection datasets. Ground cover models cannot be compared with other variable tests due to split-plot design. For the fungal collection dataset, both soil variables and parasitic mushroom models cannot be compared with other models. Only 17 of 19 sites had parasitic mushrooms present and air temperature was used as a control variable. Green cells had significant un-adjusted p-values while yellow cells have significant un-adjusted p-values and significant differences in spread.

(presence of stands predating development, native shrub effective richness, tree community typology, percent impervious surface on site, and native conifer density). Site area was significant for the total fungal community and saprobic community, however no other variables describing socio-economic gradients were significant. Of soil variables, only nitrogen concentration was significant in explaining variation in the community of collected symbiotic fungi (Table 4.3).

The best models to explain variation in fungal community composition were single variable models for the overall fungal community and saprobic and symbiotic trophic groups (variation explained 8-19%). However, for the parasitic trophic group, the best models included median 7-day average air temperature, percent impervious on site, and either tree community group or median Douglas-fir height (m). Both explained approximately 58% of the observed variation (Appendix C: Fungi).

### 4.3.6 Community response to environmental gradients

For the collections dataset 58 genera were present on at least 3 sites and met TITAN's inclusion criteria. For the NGS dataset, 1125 SVs met TITAN's inclusion criteria (Appendix C: Fungi).

#### Community response to soil gradients

For pH and the NGS dataset, approximately equal numbers of negative (z-) and positive (z+) indicator taxa were identified along the pH gradient. Both categories of indicator taxa experienced sharp changes around pH 5.5 (median filtered sum(z-) = 5.53; median filtered sum(z+) = 5.855). This synchronous change in taxa is consistent with an ecological community threshold. Additional taxa dropped out of the community in an approximately linear sequence below pH 5.0. Negative (z-) indicator taxa in the collections dataset also showed evidence of a community threshold near pH 5.3.

For percent carbon, there are more SVs associated with lower (z-) than higher (z+) % C in the NGS dataset. While negative indicator taxa exhibit a synchronous change-point and community threshold at approximately 4-5 % C, the pattern for z+ taxa is not clear (median filtered sum(z-): 4.682; median filtered sum(z+): 6.55). Results for the collections dataset was ambiguous, with only a few pure and reliable taxa associated with higher (z+) %C.

For percent nitrogen, there are also more SVs associated with lower (z-) than higher (z+) % N in the NGS dataset. At approximately 0.2% N, there is evidence of synchronous change-points for z- indicator taxa, suggesting an ecological community threshold. However, as with % C z+ taxa join the community gradually as % N increases (median filtered sum(z-): 0.22; median filtered sum(z+): 0.321). Results for the collections dataset suggest a community threshold for z+ taxa between 0.3-0.4% N, while results for z- taxa are ambiguous.

For C:N in the NGS dataset, negative (z-) indicator taxa suggest synchronous change-points and a community threshold at approximately 17 C:N (Median filtered sum(z-): 17.947). Positive (z+) indicator taxa have asynchronous changes over the environmental gradient (median filtered sum(z+): 26.967). The widely distributed changes in z+ indicator taxa span most of the range of the C:N gradient suggesting a gradual addition of taxa tolerant of high C:N values, instead of an ecological community threshold. TITAN found few pure and reliable genera from the collections dataset, though there is some evidence of a community threshold at 23 C:N.

### Community response to area

TITAN analysis of area for the collections dataset suggests that genera are added gradually as area increases, rather than exhibiting a clear community threshold.

### Community response to development and management based gradients

I used TITAN to analyze six variables describing development and landscaping actions identified as significant in PERMANOVA results. While collections data generally agrees with the NGS data, consistent limitations of low number of observations and low numbers of pure and reliable taxa in the collections dataset suggest a more conservative interpretation Appendix C: Fungi.

Along all gradients, there were more taxa associated with the less urbanized end of the gradient. There is evidence of community thresholds (multiple taxa with change points occurring simultaneously) for percent impervious on site and native conifer density and for positive indicator taxa only for median dominant Douglas-fir height and native shrub effective species richness.

For percent impervious surface on site, a synchronous change in both increasing (z+) and decreasing (z-) taxa was observed at approximately 70% impervious surface on site. Below 70% impervious surface on site there is an asynchronous distribution of decreasing (z-) taxa change points, suggesting that additional taxa drop out gradually at lower levels of impervious surface coverage. However relatively few sites were sampled between 60-70% and below 50% impervious surface; additional sampling of lower % impervious surface on site may reveal additional community thresholds at these levels.

For median dominant Douglas-fir height (m), negative (z-) indicator taxa in the NGS dataset declined gradually between 5 and 25 m (median filtered sum(z-): 19.4). In contrast, positive (z+) indicator taxa increased sharply between 27 and 37 m (median filtered sum(z+): 35.6) suggesting that there may be a defined ecological community threshold with increasing median Douglas-fir height around 35 m. The collections genera follow similar pattern as in the NGS dataset.

For native conifer density (tree/acre), negative indicator taxa (z-) declined sharply between 0-4 native conifer trees/acre for the NGS dataset, suggesting an ecological community threshold (median filtered sum(z-): 4.677 trees/acre). Positive (z+) indicator taxa exhibit two sharp inclines, the first between 22-25 trees/acre and the second between 40-50 trees/acre (median filtered sum(z+): 23.595). Plots of the sum(z) also support two discrete taxa change points. The collections genera follow similar pattern as in the NGS dataset, though the second community threshold for z+ taxa between 40-50 trees/acre is more pronounced.

For native shrub effective species richness, positive (z+) indicator taxa increased sharply between 2.5-3.5 effective species for the NGS dataset (median filtered sum(z+): 3.06 species) supporting an ecological community threshold. Conversely, negative (z-) indicator taxa dropped out in an approximately linear sequence, suggesting an asynchronous distribution of negative (z-) taxa change points (median filtered sum(z-): 1.922). The collections dataset follows a similar pattern.

### Ecological preference for stands predating development

Multiple fungal taxa preferred sites with stands predating development (Table 4.2 and Table 4.3). Only one genus in the collections dataset preferred sites without stands predating development.

Table 4.2: NGS dataset: Fungal genus associations with sites where stands predate development.

| **Taxonomy** | **Trophic Mode** | **Mean Statistic** | **Gradient** |
|---|---|---:|---|
| Leucosporidiales order | Unknown | 0.543 | Yes stands predate |
| Umbelopsis sp | Saprotroph,<br>Symbiotroph | 0.542 | Yes stands predate |
| Wilcoxina rehmii | Symbiotroph | 0.574 | Yes stands predate |
| Coniochaeta mutabilis | Pathotroph,<br>Saprotroph,<br>Symbiotroph | 0.569 | Yes stands predate |

Table 4.3: Mushroom collections dataset: Fungal genus associations with sites where stands predate development.

| **Genus** | **Trophic Mode** | **Mean Statistic** | **Gradient** |
|---|---|---:|---|
| Cyclocybe | Saprotroph | 0.577 | No Stands Predate |
| Clitocybe | Saprotroph,<br>Pathotroph | 0.612 | Yes Stands Predate |
| Xerocomellus | Symbiotroph | 0.612 | Yes Stands Predate |
| Strobilurus | Saprotroph | 0.609 | Yes Stands Predate |
| Amanita | Symbiotroph,<br>Saprotroph | 0.577 | Yes Stands Predate |
| Trametes | Saprotroph | 0.570 | Yes Stands Predate |
| Arrhenia | Saprotroph,<br>Pathotroph | 0.542 | Yes Stands Predate |

Correlation statistics for fungal taxa in both NGS and collections data suggest moderate correlation between taxa and stands predating development (Appendix C: Fungi for genera details).

### Ecological preference for tree community groups

Multiple fungal SVs and genera in both the NGS and collections dataset preferred the native tree community habitat characterized by western redcedar, big leaf maple, Pacific madrone, and red alder. Few preferred habitat in the ornamental community group, characterized by red maple (Table 4.4 and Table 4.5; Appendix C: Fungi for genera details). The different tree community groups arise from differences in land management, including tree preservation and tree and shrub planting (Dyson, 2019c).

Table 4.4: NGS dataset: Fungal genus associations with tree community typologies.

| **Taxonomy** | **Trophic Mode** | **Mean Statistic** | **Cluster** |
|---|---|---:|---|
| Cladophialophora sp | Saprotroph, Pathotroph | 0.510 | Native |
| Coniochaeta mutabilis | Pathotroph, Saprotroph, Symbiotroph | 0.510 | Native |
| Penicillium brunneoconidiatum | Saprotroph | 0.522 | Native |
| Botryosphaeriales order | Unknown | 0.522 | Native |
| Umbelopsis dimorpha | Saprotroph, Symbiotroph | 0.523 | Native |
| Penicillium jensenii | Saprotroph | 0.523 | Native |
| Acarosporales order | Unknown | 0.524 | Native |
| Umbelopsis sp | Saprotroph, Symbiotroph | 0.545 | Native |
| Wilcoxina rehmii | Symbiotroph | 0.568 | Native |
| Solicoccozyma fuscescens | Saprotroph | 0.573 | Native |
| Sagenomella sp | Saprotroph, Pathotroph | 0.625 | Native |
| Agaricales order | Unknown | 0.512 | Ornamental |

Table 4.5: Mushroom collections dataset: Fungal genus associations with tree community typologies.

| **Genus** | **Trophic Mode** | **Mean Statistic** | **Cluster** |
|---|---|---:|---|
| Marasmiellus | Saprotroph | 0.500 | Native |
| Arrhenia | Saprotroph, Pathotroph | 0.577 | Native |
| Lycoperdon | Saprotroph | 0.600 | Native |
| Gymnopus | Saprotroph | 0.620 | Native |
| Cyclocybe | Saprotroph | 0.535 | Ornamental |

Table 4.6: NGS dataset: Fungal genus associations with ground cover types where mean statistic is greater than 0.65. SeqVar XXX indicates that no information on the sequence variant is available in the UNITE database.

| Taxonomy | Trophic Mode | Mean Statistic | Substrate |
|---|---|---|---|
| Exophiala bonariae | Saprotroph, Pathotroph | 0.674 | Grass |
| Mortierella globulifera | Saprotroph | 0.665 | Grass |
| SeqVar 954 | Unknown | 0.800 | Unmanaged |
| Inocybe cincinnata | Symbiotroph | 0.761 | Unmanaged |
| Geminibasidium sp | Saprotroph | 0.755 | Unmanaged |
| Basidioascus magus | Saprotroph | 0.747 | Unmanaged |
| Exophiala sp | Saprotroph, Pathotroph | 0.702 | Unmanaged |
| SeqVar 2743 | Unknown | 0.700 | Unmanaged |
| Cladophialophora sp | Saprotroph, Pathotroph | 0.697 | Unmanaged |
| Umbelopsis sp | Saprotroph, Symbiotroph | 0.678 | Unmanaged |
| Penicillium humicoloides | Saprotroph | 0.671 | Unmanaged |
| Gomphidius oregonensis | Pathotroph, Symbiotroph | 0.654 | Unmanaged |

**Ecological preference for substrate types (NGS only)**

Sequence variants in the NGS dataset exhibited ecological preferences for the different substrate types (mulch, grass, unmanaged, and forest). Almost all preferences detected using the point biserial correlation coefficients were for sequence variants associated with 'unmanaged' habitat (Table 4.6). These areas of unmanaged remnant forest habitat on office developments were covered with dense shrubs, including salal. This result agrees with PERMANOVA analysis results finding 'unmanaged' habitat different in both location and spread. The mean statistic for sequence variants and 'unmanaged' habitat is generally medium to high (Hinkle et al., 2002).

## 4.4 Discussion

### 4.4.1 Explaining variation in effective species richness

Variation in effective species richness is explained by different variables for the NGS and collections dataset. For the NGS dataset, weighted C:N significantly explained variation effective SV richness; the model with this variable alone explained approximately 34% of variation. Previous research suggests that urban saprotrophic species richness positively correlates with available nitrogen (Newbound et al., 2012). My results suggest higher ratio of nitrogen to carbon is positively correlated with NGS effective species richness, though not with weighted N % alone.

Only the mushroom collections dataset provides support my hypothesis that woody debris availability would explain variation in effective species richness. While this aggrees with previous research, more research on the effect of ornamental mulch application in social-ecological systems is needed (Brantley et al., 2001; Bridge and Prior, 2007; Chalker-Scott, 2007; Shaw et al., 2004).

Overall, the mushroom collection dataset suggests that higher species richness is found on less disturbed sites (e.g. less impervious surface). This result agrees with research in Milwaukee, WI, which found that in general increased urbanization appeared to decrease species richness (Turnquist et al., 2016).

For both datasets, site-scale variables were more important than neighborhood-scale variables, though my study design limits these conclusions by not surveying the ends of the size and surrounding impervious gradients. Additionally, that site area was did not explain variation in effective species richness generally disagrees with previous research elsewhere, though I found no comparable studies in the Pacific Northwest. For example, a study in Sydney, Australia found a relationship between fungal species richness and measures of habitat fragmentation of remnant habitats, including patch size, perimeter to area ratio, and distance to other large reserves (Drinnan, 2005). Habitat size was also significant in road medians and urban parks in Manhattan, though less than expected (Reese et al., 2016).

### 4.4.2 Explaining variation in community composition

Variables describing soil chemistry, development actions, and land management actions were consistently significant in explaining variation in community composition for both NGS and mushroom collection datasets. However, the effect size was small for all models save parasitic mushrooms in the collections dataset. Few detection variables for the collections dataset or neighborhood-scale variables for either dataset were significant.

These results agree with other research and confirm my hypotheses that soil chemistry is an important determinant of community composition, that site-scale variables are more important to fungal community composition than neighborhood-scale variables, and that development and land management actions are more important than the measured socio-economic variables (Newbound et al., 2012). However, the importance of ground cover is ambiguous, and woody debris does not appear to be significant, failing to support those hypotheses.

Soil chemistry variables were consistently significant in explaining variation in community composition for both datasets. The two communities responded somewhat differently to measures of soil chemistry; pH and weighted C:N were significant for the NGS dataset while weighted % N and C:N were significant for the mushroom collections dataset. These results largely agree with previous research in Melbourne, Australia which found that pH, nitrogen, and carbon were significantly correlated with fungal community composition (Newbound et al., 2012). My results also agree with research on agricultural land and natural landscapes finding changes in community composition over soil nutrient gradients, including pH and N gradients (Högberg et al., 2007; Lilleskov et al., 2002; Treseder, 2004). This result suggests that soil nutrients, regardless of source influence fungal community composition.

Site-scale variables describing the outcome of development and landscaping actions were significant explanatory variables for fungal community composition for both NGS and mushroom collections datasets. In particular, the resulting native vegetation on office developments influences fungal community composition. Findings that native plants are important agree with research in Phoenix, AZ, which found the presence of native plants influenced species composition of AM fungal communities, and unvegetated sites lacked AM fungal spores (Cousins et al., 2003). Similar results were observed in the EM fungal community; in Kansas comparisons of communities on native and non-native ornamental host roots differed significantly even though species richness and diversity did not (Lothamer et al., 2014).

Site-scale variables describing maintenance activity like dead wood removal and fertilization did not explain variation in community composition for either NGS or mushroom datasets. These results are surprising and contradict univariate results for the mushroom collection dataset and my hypothesis that fungal communities would be associated with dead wood abundance; this also disagrees with previous research using other methods where rare and endangered fungi were found to be more abundant with increasing amounts of dead wood (Nordén et al., 2013).

Fertilization, particularly nitrogen addition, alters fungal communities on agricultural land (Lehto and Zwiazek, 2011; Treseder, 2004). Significant soil variables like C:N ratio and % soil nitrogen also suggest that fertilization should be important. One possible explanation is that other drivers of soil chemistry are more important than the amounts of fertilizer added, particularly as reported frequency and application amounts were relatively small. Another probable explanation is that reported behavior and actual behavior differ. This may also account for the discrepancy between stated mushroom removal and lack of impact on mushroom collections data, although field experience suggests that most people do not notice mushrooms unless they are large and brightly colored (e.g. *Amanita muscaria*).

While mulching and irrigation are significant in explaining variation in mushroom collection community composition, both have significant differences in dispersion as well as location. Irrigation is likely not important, as betadispersion plots suggest differences in dispersion but not location. However, mulching may be important as betadispersion plots for mulching suggests differences in dispersion and location. However, as there were only three sites that were not mulched, the sample size is too small to say for sure.

Ground cover type was used to stratify sampling for the NGS dataset based on previous research suggesting ground cover influences fungal communities (e.g. Trinder et al., 2009). After controlling for site, I found ground cover was significant, though betadispersion plots suggest differences in dispersion and location. Specifically, mulch and grass cover showed substantial location overlap and similar dispersions, however the unmanaged ground cover type showed differences in both location and dispersion that were supported by Tukey tests. The relatively small sample size of unmanaged ground cover means that these results are ambiguous.

Few socio-economic variables were significant. In general, this agrees with other studies, though they used different metrics for neighborhood socio-economic variables (Newbound et al., 2012). It also supports my hypothesis that development and land management variables resulting in altered vegetation communities would be more important than socio-economic variables for explaining community composition. Site area was significant for total and saprobic mushroom collection data, while assessed land value per acre was significant for symbiotic SV. These sparse patterns suggest that another, unmeasured, variable may be responsible. For example, land rent may be tied to another variable such as a location- or amenity-based economic variable (though not percent impervious or area).

Comparisons with other studies are complicated by the imprecise measures of 'degree of urbanization' in urban fungal literature. For example, researchers in Wisconsin found that neither degree of urbanization nor intensity of landscape management altered fungal community composition, however both of these were characterized only by land use, relative age, and a qualitative intensity designation (Turnquist et al., 2016). Research in Manhattan also found that land use did not impact fungal community composition (Reese et al., 2016). These studies may have found different patterns of fungal community composition than my research–or it may be a matter of different uses and measures of 'urban' (McIntyre et al., 2000). Future studies should use more precise and ecologically relevant definitions; land use (e.g. 'residential') is remarkably heterogeneous, and qualitative measures cannot be easily replicated.

A key exception is that variation in symbiotrophic fungi was not explained by the same variables as other trophic subsets. This could be due to the use of aggregated measures of the vegetation community (native conifer density) instead of presence or density of specific vegetation species. This requires further study.

Lack of consistency in collection methods is a barrier to comparing my research with previous research for both univariate and multivariate methods. Collection methodologies include NGS soil samples (this study), counting spores in soil samples (Cousins et al., 2003), sequencing mycorrhizal root fungal communities (Lothamer et al., 2014), and mushroom collection surveys (Drinnan, 2005). More consistent methodologies, including comparing different methodologies in laboratory and real world settings would aid our understanding of urban fungal communities.

### 4.4.3 Response of fungal taxa to environmental gradients

This study marks the first use of TITAN in urban fungal research. Comparisons with studies performed in other ecosystems suggests that the proportion of SVs observed with significant *p*-values compares favorably with other studies (Chariton et al., 2015; Jassey et al., 2018), though cutoffs for pure and reliable taxa criterion for these studies were not reported.

Correlation indices and TITAN produced consistent results. For both analyses and datasets, no taxa were associated with the "less disturbed" end of one environmental gradient and the "more disturbed" end of another. For example, in the mushroom collections dataset, genera associated with "native" tree vegetation clusters (e.g. *Lycoperdon* or *Arrhenia*) were also associated with the "less disturbed" ends of the native conifer density land management environmental gradient, and vice versa (e.g. *Cyclocybe*). Additionally, multiple genera, including *Xerocomellus* and *Amanita*, were identified as z+ taxa in TITAN for both datasets. This provides additional support for both analyses, as two datasets measuring different portions of the fungal community resulted in similar statistical outcomes.

Evidence for community thresholds are present for most variables. All soil gradients including pH, % C, %N, and C:N, along with all development and management gradients including % impervious on site and native conifer density, median dominant Douglas-fir height and native shrub effective species richness for at least one taxonomic indicator group (increasing/z+ or decreasing/z-), though not site area. However, identifying change point location is hampered by relatively sparse sampling.

While results from these analyses are generally interpretable and consistent, more questions remain. First, most sequence variants in the NGS dataset with substrate ecological preferences were associated with the 'unmanaged' habitat. Results from PERMANOVA and beta dispersion tests of ground cover suggest the 'unmanaged' ground cover habitat differs in both multivariate location and spread. Whether these results support each other–that is, that the unmanaged habitat is truly unique in some way–or are the result of a measurement error is unknown and additional study is required. Second, there are few additional studies to compare these results with. Finally, patchy site distribution for multiple environmental gradients and poor sampling of the entire (potentially very long) gradient means that we cannot dismiss the potential presence of other thresholds (King and Baker, 2014).

### 4.4.4 Overall patterns of fungal communities on office developments

The three methods (univariate and multivariate PERMANOVA and TITAN) are complimentary and allow examination of multiple aspects of the fungal community. Generally, the multivariate methods (PERMANOVA and TITAN) agree, while a slightly different set of variables was found significant with univariate methods. This discrepancy suggests that studies reporting univariate and multivariate measures of fungal communities may not be directly comparable. Multivariate methods, which preserve taxonomic identity, may be more important for ecosystem function and service provision in socio-ecological systems.

Overall, I conclude that many SVs are adaptable to environmental gradients in social-ecological systems, distributed across the landscape stochastically, and/or distributed in response to patterns and processes not measured in this study. I come to this finding based on the relative lack of response in effective richness to social and ecological gradients and that most of SVs are not pure and reliable taxa for TITAN. Stochastic assembly processes explained beta-diversity in soil mite populations (Caruso et al., 2017) and may for fungi as well (Lekberg et al., 2011). Other researchers have found little overlap in community composition between different sites in natural systems (Karpati et al., 2011). Fungi may also be more resilient to disturbance than previously thought; for example, disturbance did not significantly alter AM fungal community composition or species richness in grasslands ecosystems (Lekberg et al., 2011).

However, there are some taxa with a strong response to environmental gradients measured here, including soil chemistry (pH, C:N, %N), and development and landscaping gradients describing the native tree and shrub community and percent impervious on site. For these fungi, site-scale variations in habitat are likely more important than neighborhood-scale variations.

### 4.4.5 Research limitations and strengths

This research is limited both by constraints in fungal taxonomic databases and study design. Databases like UNITE are incomplete, and many sequence variants identified here and elsewhere are not associated with known fungal taxonomy (Hibbett et al., 2016). Significant work remains to match DNA to taxonomy and function (Nagy et al., 2011; Truong et al., 2017).

There are two important implications of fungal database limits for this and other research. First, what type of diversity is technically being measured depends on analytical choices which make it hard to compare between studies. Some studies use taxonomic information from UNITE to agglomerate to genus level and then drop 'unknown' SVs/OTUs (e.g. Karpati et al., 2011). This eliminates a large portion (>50%) of the dataset based on the arbitrary criteria of whether a sequence can be database matched to a taxonomic identification. It also creates disparate aggregation levels where some unidentified sequences may be a genetic variant of an aggregated species, effectively double counting those species. Further, different rates of study and sequencing of fungal taxa means that certain lineages—including understudied and difficult to culture fungi—are under-represented in UNITE and other databases. Any agglomeration will misrepresent the relative importance of these taxa. As a result, agglomerating based on matched taxonomy is methodologically and ecologically unsupportable. However, the alternative is technically measuring genetic diversity instead of taxonomic diversity, as I did here. Genetic diversity includes any difference in sequence, including genetic variations within species.

Second, database limitations mean that I could only include a subset of SVs in trophic guild analysis, as many could not be identified to genus and therefore could not be assigned to a trophic guild. Unlike with the agglomeration discussed above, this cannot be avoided. Trophic guild analyses are therefore biased towards species that have been successfully cultured or collected and sequenced (Hibbett et al., 2016). How biased this subset is cannot be easily assessed. The mushroom dataset avoids these limitations, which partially helps this study mitigate bias with the NGS dataset (Hart et al., 2015). However, collections miss yeasts, molds, and species that rarely fruit, which are important to ecosystem functioning (Rodriguez et al., 2009).

Additionally, limits in our current understanding of the ecological role specific taxa constrains our ability to interpret observed patterns in the distribution of taxa across urban gradients. Most fungal taxa that were identified to genus or species can be classified according to trophic guild (saprotroph, symbiotroph, pathotroph), though this classification sometimes relied on reports of where taxa were observed (e.g. *Valsonectria pulchella* is found on wood of *Melia* sp. Seifert and Samuels, 1997). However, information on niche, decomposition pathways, preferred pH, preferred soil strata, etc. was difficult to obtain for all but the most well studied species. Further, our ability to identify parasitic fungi appears much more limited than our ability to detect saprotrophic or symbiotrophic species. The only alternative to relying on taxonomic based function information is to directly measure function in future studies.

This research is also limited based on study design. My fairly small sample of 17-19 office developments provides statistical power limitations. More complete sampling along social environmental gradients is also required to better understand fungal community response to complex social-ecological systems (Dyson, 2019c). However, by stratifying along a vegetation gradient I was able to identify trends in fungal diversity related to development and landscaping actions. Additional sampling between land uses is also needed. If management intensity varies between land uses (e.g. residential property nutrient input may be higher; Fissore et al., 2012) I expect more fungal taxa to be impacted by environmental gradients resulting from ecosystem process.

Finally, differences between my study and other research may come from methodological differences. For example, while Drinnan (2005) used similar fungal mushroom collection methods, Barrico et al. (2018) and Turnquist et al. (2016) used PCR gels instead of NGS techniques. Additionally, these studies examined remnant habitat and urban parks, not developed parcels, and used species richness instead of effective species richness (although these measures are generally fairly similar). Others looked at limited sub-sections of the fungal community; Karpati et al. (2011) examined EM fungal communities only on *Quercus rubra* (northern red oak).

### 4.4.6 Policy implications and guidance for land managers

Patterns found in this research combined with previous research and ecological theory provide some policy implications and guidance for city and land managers. Importantly, creating local reserves and restoring degraded habitat are important but incomplete responses to habitat loss, and implementing changes to the management of the urban matrix is necessary for conservation efforts to be successful in urbanizing regions (Goddard et al., 2010; Miller and Hobbs, 2002; Rosenzweig, 2003). Actions at the parcel-scale contribute collectively to the habitat available in the broader urban matrix.

Overall, the best approach for city and land managers to take is to follow the precautionary principle. Practically, this would mean writing policy at the city level and acting at the parcel level to avoid unnecessary impacts on the existing fungal community and preventing infection vectors for pathogenic and invasive non-native fungi.

Development action outcomes are important for a subset of the fungal community; these include tree and shrub preservation, soil disturbance during site clearing and grading, and impervious surface installation. Tree and shrub preservation influences host plant availability and alters fungal community composition (this research; Cousins et al., 2003; Lothamer et al., 2014). Ideally, cities would implement tree protection policies which are ecologically meaningful—however city codes may be ineffective and/or include perverse incentives (Seattle, 2017). This also preserves nearby soil, creating reserves for fungi during development; policies reducing soil disturbance during site clearing and grading may also reduce change in fungal community composition. Policy impacting percent impervious surface on site, including parking lot requirements in zoning code will also impact potential habitat area. Impervious surface policy impacts habitat fragmentation, soil properties, and runoff pollution, which may also be mechanisms of fungal community change (Davis et al., 2010).

Choices made after development, including landscape design choices and ground cover choices, are also likely important for a subset of the fungal community. Key policies actions include substituting natives for non-natives on tree planting lists, which frequently feature deciduous species from eastern North America, Europe, and Asia, and encouraging native shrub planting (Cousins et al., 2003; Lothamer et al., 2014). Using native plants in urban areas is important to maintain native fungal communities—and for the continued success of native plants (Corbin and D'antonio, 2012; Lothamer et al., 2014). More research is needed to see if choosing to retaining downed logs and snags may be beneficial for fungal conservation (Dove and Keeton, 2015; Juutilainen et al., 2016; Komonen et al., 2014; Runnel et al., 2013).

Finally, reducing potential vectors for high-risk pathogenic fungi and non-native invasive fungi is prudent. In the Puget Sound region, logging activities between 1880-1920 likely contributed to the spread of laminated root rot (caused by *Phellinus sulphurascens* in Douglas-fir). Development activities have the potential to do the same via transport of topsoil containing infected root tissue. Encouraging construction hygiene, including reducing direct damage to tree trunks and roots by ensuring that dripline protection is sufficiently large, and reducing movement of soil with potentially infected woody material between sites are important measures. Further because we know little about which species are non-native and possibly invasive, it is prudent to pay attention to and research potential vectors including mulch, fungal inoculation at nurseries, and soil movement (Ammirati, personal communication).

### 4.4.7 Contributions and future research needs

Less is known about urban fungi than higher taxa from systematic study. As a result, this work on fungi is more exploratory than the concurrent vegetation and bird research conducted on office developments (Dyson, 2019c, 2019a). This study identifies multiple processes in social-ecological systems influencing fungal community composition, provides guidance for policymakers and land owners.

These results also point to important avenues for future urban fungal research, including observational, longitudinal, and manipulation studies that should be done. Access to private property to conduct these experiments remains a concern and constraint for future research (Dyson et al., 2018).

Taxonomic responses to social and environmental gradients in urban ecosystems should be further explored. In addition to more complete studies of those gradients addressed here, land use history legacy effects (Karpati et al., 2011), more complex soil chemistry variables (e.g. Dini-Andreote et al., 2016), and soil age instead of building age (Chaudhary et al., 2018; Dini-Andreote et al., 2016; Francini et al., 2018) are areas for future research. Variables measured here using interview responses instead of direct measurement should be more accurately measured and tested.

Future research must be sure to sample the entire gradient. Some social variables measured in this study may not be significant simply because I could not sample their entire range due to relatively small sample sizes (King and Baker, 2014). However, because I used stratified random sampling based on vegetation instead of simple random sampling the vegetation gradient was well sampled. A random sample would have resulted in a subset of many important site-scale variables including native conifer abundance and presence of stands predating development (Dyson, 2019c).

Direct measurements of fungal function—including litter bag tests, mycorrhizal colonization experiments, and soil enzyme activity—are needed to understand how ecosystem services and disservices are impacted by social-ecological ecosystem processes (Jassey et al., 2018). How the relationship between fungal species and their hosts changes across social and ecological gradients for both mycorrhizal and pathogenic species is another important area of study. The higher risk profile of urban areas increases the importance of research into mapping urban hazards, early hazard tree detection, and tree susceptibility to pathogens.

Many basic questions about fungal communities in urban areas remain unanswered. This research found a new forma, and there are certainly additional species and forma to be found in urban areas. Basic fungal research are necessary to determine ranges for species and whether species are native or introduced.

Little is known about fungal dispersal or how much spores contribute to fungal dispersal and colonization, though it likely varies significantly by taxa (e.g. *Armillaria* vs. *Phellinus*). Long term, geographically diverse datasets of fungi are required to determine ranges and preferred habitat for fungi and build up a more accurate picture of key processes including dispersal and invasion (Jumpponen and Egerton-Warburton, 2018). Ongoing data collection should include mushroom collection, culturing, and sequencing to continue adding to the UNITE database and the broader fungal taxonomy. Many of the range-based ecological approaches taken for granted in mammalogy, ornithology, etymology, and botany cannot be meaningfully applied in mycology.

Methodological comparisons are needed to better compare existing and future studies; this includes comparing how NGS pipelines (OTU vs dada2) and aggregation approaches alter study conclusions. Comparing the results from appropriate multivariate techniques with univariate approaches may reveal that univariate techniques obscure changes in community composition along environmental gradients (this research; King and Baker, 2014). If there are differences in outcomes based on processing pipelines, aggregation approaches, or if studies have relied on univariate approaches, there is convincing argument to be made for reanalyzing older datasets collected under well-conceived sampling designs employing improved statistical techniques (Callahan et al., 2016).

These questions only scratch the surface of how much research remains to be done on urban fungi. Continuing research to determine ecosystem processes which alter the distribution and function of fungi in urban areas is necessary to conserve fungi in cities (Newbound et al., 2010). Interdisciplinary research with the social sciences into city and land manager motivations and preferences may also provide important conservation insight but is outside the scope of this study.

## 4.5 Conclusions

Development, landscaping, and maintenance actions alter urban habitat by altering vegetation communities, changing habitat area and fragmentation, and modifying soil chemistry (Batten et al., 2006; Newbound et al., 2012, 2010). Using NGS and collected mushroom specimens, I found that parcel-scale development and landscaping actions which altered soil chemistry and nutrient availability, native tree density, tree community composition, shrub richness, and percent impervious surface explained variation in observed fungal community composition, but with few exceptions not effective species richness. There were also ecosystem community thresholds associated with many of the environmental gradients resulting from development and landscape design actions.

Overall, many fungal taxa found on office developments in Redmond and Bellevue, WA are adaptable to gradients in socio-ecological systems, distributed across the landscape stochastically, and/or distributed in response to patterns and processes not measured in this study. However, a group of fungal taxa have a strong response to environmental gradients resulting in part from human action. Most of the taxa in this group are positively associated with “less disturbed” ends of the urban environmental gradients and exhibit change points that contribute to evidence for ecosystem community thresholds. These thresholds suggest changes in ecosystem function provided by fungi across the gradient, however we do not have enough information about function provision by individual fungal taxon to draw firm conclusions. Future urban fungal research should explicitly measure ecosystem process across the gradients identified here. The paucity of urban fungal research generally makes this research more exploratory in nature than other chapters in this dissertation. How generalizable these results are is uncertain and possibly variable.

Based on these results and that comparatively little is known about the response of urban fungi to socio-ecological system processes, the best approach for city and land managers to take is to follow the precautionary principle. Policy and actions that avoid unnecessary impacts on pre-existing fungal communities, encourage native tree and shrub communities, and prevent vectors for pathogenic and invasive non-native fungi are prudent. These parcel-scale actions in the urban matrix can contribute to landscape-scale connectivity and habitat provision and help to support conservation at broader scales (Fahrig, 2001; Fischer et al., 2006; Goddard et al., 2010; Miller and Hobbs, 2002; Polasky et al., 2005; Rosenzweig, 2003)

# Chapter 5

# Urban ecology helps support urban policy and action

In 2000, Timothy Beatley suggested that a new paradigm for conservation was needed—one leveraging land use planning and the participation of cities for conservation strategies that were more proactive, bolder, and larger in scale (Beatley, 2000). Almost 20 years later, urbanization and sprawl is still a major threat to biodiversity and healthy ecosystem functioning (Elmqvist et al., 2013). Urban planners, designers, and community members' concerns include loss of characteristic and place-defining native tree species, loss of native biodiversity, and reduced ecosystem services like stormwater interception. Human actions such as cutting down established trees, removing shrubby vegetation, and planting introduced landscaping are contributing factors.

Recent advances in *urban ecology* provide support for effective actions and policies that landowners, urban planners and designers, landscape architects, and concerned communities can implement to support their biodiversity and ecosystem function goals. Urban ecologists study the relationship between organisms and their habitats in cities, suburbs, and exurbs.

As an urban ecologist, I recently completed a multi-year study of office developments near Seattle, Washington. I wanted to learn whether different development and landscaping activities lead to different tree and shrub vegetation communities on office developments. I also wanted to see if this impacted what species of birds I found there.

I chose to study these organisms as in addition to their intrinsic value, trees, shrubs, and birds are important to humans and for healthy ecosystem functioning. Trees and shrubs provide most of the habitat available to other organisms, mitigate heat islands, lower rainfall runoff and flooding, reduce urban noise, provide economic benefits for property values and commercial businesses, and are responsible for landscape aesthetics important to community identity (Nowak and Dwyer, 2007; Rašković and Decker, 2015; Sullivan and Lovell, 2006). Many municipalities have tree protection policies and canopy cover goals for these reasons. Birds are used as indicators of biodiversity globally, eat pests, pollinate flowers, and disperse seeds. They also are charismatic and provide cultural ecosystem services important to a large number of residents (Belaire et al., 2015; Blair, 1999). While what constitutes ecological health depends on social values, these ecosystem services provide significant value to human communities (Tzoulas et al., 2007).

As might be expected, I found that decisions about vegetation clearing and grading activities determined what trees will survive development. In Seattle, there is a wide range of post-construction landscapes, including office developments with many surviving large trees and those with very few. I also found that decisions about landscape planting determines the tree and shrub species at a development, with the remnant trees and shrubs surviving clearing and grading activities. Developed parcels differ in the number of trees and shrubs present, and whether these species are native or introduced to the area.

I found two patterns in trees and shrubs on an office development that positively impacted bird biodiversity and ecosystem function. First, preserving large native conifer trees is beneficial, and second, planting native trees and shrubs is beneficial. Both results are supported by other research and can be translated into evidence based actions and policies.

I first discovered that office developments where more large native conifers survive development were positively correlated with the total number of bird species. Native conifers provide important food and shelter and include Douglas-fir, western redcedar, and western hemlock. Popular native forest birds like Red-breasted Nuthatch and Brown Creeper were found more often where these trees were preserved. Birds that eat insects were also more common. These birds provide important cultural resources and insect control services.

Other ecologists have found the same pattern on parks and residential property (Belaire et al., 2014; Chong et al., 2014; Stagoll et al., 2012). Large trees provide critical opportunities for foraging, nesting, and perching, and are more beneficial than newly planted replacement trees (Sung, 2012). Because these trees take so long to grow, removing large trees removes ecosystem services that cannot be replaced in our lifetimes.

Urban ecology research supports implementing size-based tree protection actions and policies during and after construction in historically forested areas like Seattle (Barth et al., 2015; Shryock et al., 2017). While developing properties explicitly to preserve trees can be more complex than clearing and grading the entire site, it is feasible to develop functioning commercial properties that preserve significant numbers of existing trees. For example, one build to suit commercial development in my study was able to conserve the majority of their large native conifers by altering the building's shape and placement on the property to avoid tree removal. Strategic pathing of heavy machinery reduced the area of soil compression to retain soil structure and protect tree roots.

Size classes should be tailored to local tree species when implementing scaled penalties or rewards for conserving larger trees. For example, conifers generally grow more slowly than deciduous broadleaf trees. Tree protection policies with a blanket 8 inch diameter-at-breast-height protection cutoff will not protect conifers until they are significantly older than equivalently sized broadleaf trees. Dripline protection to avoid soil compaction near roots is another good policy step, accounting again for species-specific growth patterns. After development, large trees are often cut down for risk management. Alternative risk strategies should be explored, including fencing, site and landscape design, and strategic building reinforcement.

Urban ecology research also supports planning for future large forest canopy by planting and conserving smaller native trees today. It takes decades for saplings from nurseries to become mature trees providing cultural, habitat, and other services. Current practices are removing large tree habitat faster than it is being replaced. Along with tree protection and care, increasing native tree planting can reverse this trend (Ettinger et al., 2017; Le Roux et al., 2014).

The second thing I learned was that more bird species were present on sites with higher densities of native conifer species. Additionally, I observed more birds foraging on sites with higher densities of native conifers and greater diversity of native shrubs species. These results agree with other urban ecology studies in multiple climates (Burghardt et al., 2009; Lerman and Warren, 2011).

Introduced vegetation does not support the same biodiversity of birds, their insect prey, or other organisms (Faeth et al., 2011; Narango et al., 2017).

Urban ecology results support planting native species in landscapes. Updated tree and shrub planting lists and outreach programs can encourage planting native trees and shrubs. Suggested tree lists should be revised to include more locally native species and to remove over-represented genus. In the United States, many lists are currently dominated by Asian and European species. Eastern United States species, while appropriate on the east coast, are introduced to the western mountains and coast. Current lists include many *Acer* (maple) and *Prunus*/*Pyrus*/*Malus* (flowering plums, pears, and apples) species. Planting many of the same genus increases the urban forest's susceptibility to pests and diseases. The City of Portland, Oregon provides one example of limiting planting of abundant genus like Acer (https://www.portlandoregon.gov/trees/article/516341).

Existing land use regulations can encourage planting decisions favoring non-native species. When revising codes, consider the unintended impacts of land use regulations on biodiversity and ecosystem service provision. For example, minimum parking space requirements dictate area required for parking spaces and can limit landscaping configurations (DeLaria, 2008; Environmental Protection Agency, 2011). A build to suit landowner in my study expressed frustration that parking lot requirements precluded planting large trees and instead encouraged multiple small trees with less habitat and stormwater interception potential.

Actions and policies to protect large trees and plant native tree and shrub species contribute to biodiversity and valuable ecosystem services, economic benefits, and aesthetic benefits. Partnering with urban ecologists in your region can help develop new approaches to local issues—such as balancing tree preservation with development pressures, social equity, and risk from global climate change.

In the end however, education, outreach, creating additional policies, and ensuring compliance with policy can only be a partial measure. Landowners must actively choose the ethical responsibility of managing their land.

> "There is a clear tendency in American conservation to relegate to government all necessary jobs that private landowners fail to perform.... A system of conservation

based solely on economic self-interest is hopelessly lopsided. It tends to ignore, and thus eventually to eliminate, many elements in the land community that lack commercial value, but that are (as far as we know) essential to its healthy functioning.... It tends to relegate to government many functions eventually too large, too complex, or too widely dispersed to be performed by government. An ethical obligation on the part of the private owner is the only visible remedy for these situations." (p213-214; Leopold, 1989)

# Chapter 6

# Research summary and conclusions

Here, I asked "*What outcomes of human actions in urban ecosystems explain variation in community composition present on office developments?*" I focused on the outcomes of human actions taken at the parcel-scale, including actions taken during development, landscaping, and site maintenance. I compared these with neighborhood- and parcel-scale socio-economic variables and neighborhood-scale land cover variables describing patterns found significant in other research (Heezik et al., 2013; Lerman and Warren, 2011; Loss et al., 2009; Munyenyembe et al., 1989). I tested how well the outcomes of these actions explained variation in patterns of vegetation (Chapter 2), bird (Chapter 3), and fungal (Chapter 4) community composition.

## 6.1 Research contributions

My research represents some of the only research on commercial developments, urban winter bird communities, and urban fungal communities (Bourne and Conway, 2014b; Newbound et al., 2012; Snep, 2009). It contributes both to our knowledge of urban ecosystems and our understanding of how human actions may be altered to better support conservation goals.

Two main groups of findings add to our knowledge of urban ecosystems. First, I found that observable outcomes of human development and landscaping action are related to differences in tree and shrub communities. In Chapter 2, I found that there are distinct planting patterns on office developments, and there is significant variation in woody vegetation, particularly in tree communities, between office developments. This variation is explained by different development and landscaping actions. Specifically, I found:

- There are two distinct planting patterns on office developments: a native and an ornamental typology for the tree and shrub communities. I observed that native trees and shrubs are frequently found together and that ornamental trees and shrubs are frequently found together. This pattern is the outcome of developer's choices to preserve existing native trees, and ongoing actions from the land owner to continue to preserve these trees. These observations also suggest that landscape designers tend to plant native shrubs where there are also native trees preserved, though why is unknown.
- Native tree communities were associated via NMDS plots with the presence of taller, older, and more abundant native conifer species. Native shrub communities were also correlated via PERMANOVA with native tree communities and taller, older, and more abundant native conifers. In contrast with studies performed on residential properties, variation in tree and shrub communities was not explained by any of the neighborhood or site-scale socio-economic variables (Clarke et al., 2013; Hope et al., 2003; Leong et al., 2018). Maintenance actions including irrigation and fertilization also did not explain variation in tree and shrub communities.

Second, I found that these differences in vegetation community composition—and particularly tree community structure—are correlated with differences in bird and fungal community composition. In Chapter 3, I found that woody vegetation patterns resulting from development and landscaping actions explained variation in bird effective species richness and community composition. Specifically, I found:

- Bird species richness was significantly explained by and positively correlated with variables describing development and landscaping actions to preserve communities of older, larger, native conifers and negatively correlated with greater % impervious coverage. Bird community composition was also explained by these variables, along with other variables describing development and landscaping actions: the density of native conifers and for foraging birds only, the effective species richness of native shrubs.

- Variables describing maintenance actions, along with neighborhood and site-scale socio-economic variables and neighborhood-scale land cover variables were not significant in explaining variation in either bird or foraging bird effective species richness or community composition. This agrees with some, though not all, studies of bird communities on other land use types, suggesting additional multi-city research with standard methods and year-round observations are necessary (Belaire et al., 2014; Daniels and Kirkpatrick, 2006b; Galitsky and Lawler, 2015; Lerman and Warren, 2011; Luck et al., 2013; Melles et al., 2003).
- Birds on office developments had similar vegetation preferences as has been observed elsewhere; for example conifer associated native bird species were associated with native tree communities on office developments. This agrees with other studies finding that native bird species were disproportionately associated with native vegetation (Burghardt et al., 2009; Lerman and Warren, 2011).

In Chapter 4, I found that woody vegetation patterns resulting from development and landscaping actions explained variation in fungal community composition in both next-generation sequencing (NGS) and mushroom collection datasets, though fungal species richness was less clear. Specifically, I found:

- Variation in fungal community composition was explained by variables describing development and landscaping actions including tree and shrub community group, the presence and abundance of old, large, native conifers, and how much impervious surface was present on site, as well as by variables describing soil pH, carbon to nitrogen ratio, and concentration of carbon and nitrogen.
- Variables describing maintenance actions generally did not explain variation in community composition; these may relate to C:N ratios but the link between fertilizer and C:N is not well established in this research. As with woody vegetation and bird communities, and agreeing with other urban fungal research, neighborhood and site-scale socio-economic variables and neighborhood-scale land cover variables did not significantly describe fungal community composition (Newbound et al., 2012).
- Community response to environmental gradients (e.g. few to many large conifers) revealed

that some taxa exhibited strong, consistent responses with evidence for community thresholds. However, most taxa are stochastically distributed or responding to other gradients. Urban fungi remain a new area of research with many avenues for future study.

Overall, I found that variables describing the outcome of development and landscaping actions were associated with tree community composition and explained variation in the community composition of shrubs, winter passerine birds, and fungi on office developments. Variables describing native tree size and abundance—including the presence of stands predating development, median height of dominant Douglas-fir, and native conifer density—were consistently significant for shrub, bird, and fungal communities and their respective trophic groups. For all three taxonomic groups, site-scale variables describing these outcomes were more important than neighborhood-scale socio-economic or land cover variables.

My research also contributes to our understanding of how human actions may be altered to better support conservation goals. To inform policy and guide landowner actions to effectively achieve conservation goals, we need to understand relationships between human action, ecosystem processes, and landscape patterns of community diversity and composition in urban ecosystems. Providing sound ecological advice is necessary as our understanding of how to manipulate the built environment in order to support conservation is in its early stages (Chapman et al., 2017). My finding that different development and landscaping actions impact urban ecosystems in meaningful ways suggests that there is the potential to design the built environment matrix to support larger populations of species, including native bird and fungal taxa in the Puget Trough. This should help reduce local extinction as larger populations are less susceptible to extinction from stochasticity and thus contribute usefully to conservation in urban ecosystems, including on office developments (Rosenzweig, 2003, 2001).

My results suggest development and landscaping actions to take and policies to implement to support conservation which I describe in Chapter 5. Most importantly for land managers, city planners, and others interested in conservation is the prudent preservation of native conifer forests wherever compatible with land use. Specifically, these groups should consider:

- Implementing size-based species specific tree protection actions and policies during and after construction. This includes implementing tree protection policies with increasing penalties or rewards for conserving larger size classes of important native tree species. Size classes and dripline protections should be tailored to the unique ecology of local tree species.

- Planning for future forest canopy by planting and conserving smaller native trees. It takes decades for saplings from nurseries to become mature trees providing cultural, habitat, and other services. Land managers, city planners, land owners, and others must therefore consider the need for planting or allowing recruitment of young trees to facilitate succession processes to maintain native conifer forest habitat for the benefit of future birds, fungi, and human residents.
- Planting native tree and shrub species in landscapes via updated tree and shrub planting lists and outreach programs. Suggested tree lists should be revised to include more locally native species and to remove over-represented genera. More broadly, when revising codes consider the unintended impacts of land use regulations on biodiversity and ecosystem service provision.

Taking actions to support conservation may also have broader impacts on the social-ecological system than what can be supported here. Other studies have shown that more native vegetation is correlated with greater proportions of native insects (Crisp et al., 1998; McKinney, 2002), while non-native ornamentals are unlikely to support the same species, biomass, or diversity of fauna (Burghardt et al., 2009; Faeth et al., 2011; Jellinek et al., 2004; Rebele, 1994). Vegetation may also provide ecosystem services benefiting humans, including mitigating urban heat islands and air quality, lowering stormwater runoff and flooding, and reducing urban noise (Nowak and Dwyer, 2007) along with economic benefits for property values and commercial businesses (Orland et al., 1992; Rašković and Decker, 2015) and aesthetic benefits (Sullivan and Lovell, 2006). Bird species richness is potentially correlated with the richness of other taxonomic groups, including butterflies (Blair, 1999), and is also correlated with people's perception of nature (Belaire et al., 2015). Fungi also provide important ecosystem services, including decomposition (Blanchette, 2000) and mycorrhizal formation (Reynolds et al., 2005; Van Der Heijden et al., 2017). While what constitutes ecological health depends on social values, these ecosystem services provide significant value to human communities (Tzoulas et al., 2007).

## 6.2 Research limitations and generalizability

There are three important limitations on my research. My research results are data limited by a relatively small number of study sites (17-20 office developments) with data collected over a relatively short period of time. As in many other ecology studies, the number of study sites and therefore statistical power was limited by practical constraints of time and personnel, and additional sites and years of data collection would improve statistical power (Sutherland, 2006). Despite small sample size and short duration, this study represents some of the only research on commercial developments, urban winter bird communities, and urban fungal communities.

I used disproportionate stratified random sampling. My method of sampling results in more sites from the ends of the gradient of vegetation on office developments than would happen with simple random sampling. This may complicate generalization and calculation of population level metrics. However, this method of sampling is the only way to ensure that the ends of the gradient are adequately sampled. If I had taken a simple random sample of office developments, I would have sampled an incomplete gradient of important site-scale variables including median dominant Douglas-fir height, and many of these variables would not have been significant in PERMANOVA or revealed synchronous change points indicative of fungal community thresholds.

I restricted the sampling pool to sites in the 25th to 85th percentile for size and the 15th to 85th percentile for surrounding impervious surfaces. This was done to remove potential confounding variables, specifically site area and area of preserves in the surrounding area. While covering the majority of sites, this decision limits my ability to detect significant relationships between community composition on site and the ends of these environmental gradients.

Finally, the socio-economic variables chosen based on previous studies insufficiently described commercial property. While residential neighborhoods surround almost all of my research sites, the diversity of agents in social-ecological systems means that what is important for residential vs. commercial properties also differs. Better measures of non-residential land uses is needed for future research.

I expect results for all taxa to hold for office developments in Bellevue and Redmond, and those in the broader Puget Trough region if they fit the limits of sampling design (constraints on size and percent impervious surface within 500 m). My results may not be generalizable outside these limits. Certain results, including winter passerine bird habitat associations, confirm existing knowledge and may extend more broadly to other land uses (e.g. residential) and the Puget Trough urban landscape more generally. These results may not be generalizable beyond the Pacific Northwest west of the Cascades and elsewhere, as there are important differences here in native woody vegetation, passerine, and fungal communities, and the broader biogeophysical and social ecological systems context. These may include different patterns in development and aesthetic preferences in landscaping.

## 6.3 Future research directions

My findings, along with the limitations of my research, provide many suggestion for future research. I identified taxon specific research needs in Chapters 2, 3, and 4. Some specific ideas include:

- Expanding on my results by examining sites across the entire gradient of surrounding impervious surface and/or size while holding on-site vegetation more constant to better test local vs. surrounding vegetation impacts.
- Landscaping choices are shaped by human preference, nursery availability, and plant survival and replacement of dead plants by landscapers; future research should explore tree and shrub planting preferences (Tenneson, 2013) and nursery availability (Torres-Camacho et al., 2017). More generally, the reasoning or decision pathways developers, property owners, and others use prior to taking actions that result in the vegetation communities I observed are still unknown. What motivates conservation or destruction of native conifers, and are local policies successful in incentivizing tree preservation? Why are native trees and shrubs planted together?
- The mechanisms resulting in different bird and fungal community composition on sites with more old, large conifers is also unknown. Measures of foraging and breeding success on commercial and other urban land uses are also needed (though see Narango et al., 2017). Researchers should also pursue multi-taxa studies to explore how community interactions

change along ecological gradients, including altered food webs and biodiversity (e.g. Faeth et al., 2011).

My research also has important implications for the methods that should be used more broadly in urban ecology research. First, the significant heterogeneity I found within the office development land use suggests the need to evaluate heterogeneity within all land use classes and casts doubt on the results from studies which compare different land uses using small sample sizes (e.g. Blair, 1999). My results show that there can be substantial variability in vegetation communities within a single land use type. Researchers should recognize that assuming a small number of sites represents the entire land use is potentially dangerous and may lead to incorrect conclusions (McIntyre et al., 2000). Understanding the underlying variability in vegetation communities within land uses is critical to our understanding and interpretation of ecological differences in studies comparing land uses and for studies of higher trophic levels in urban environments. Most urban ecology studies examining the vegetation and bird communities do not stratify across a vegetation gradient (Lerman and Warren, 2011; Loss et al., 2009) and may miss important parts of the urban ecological gradient.

Second, land uses almost certainly respond to different socio-ecological drivers. For example, residential properties may respond to socio-economic signals while commercial developments do not; the underlying motivator is likely who the intended ‘audience’ of the property is, as homeowners are signaling to their neighbors while office developments are signaling to prospective and existing tenants (Cook et al., 2012; Laverne et al., 2003; Nassauer et al., 2009). This mismatch in vegetation community response to specific variables means that urban ecologists cannot assume that the same variables explain variation for all land use types equally. Each land use type may need to be modeled independently.

Third, univariate methods may be inadequate for detecting important changes in community structure (Belaire et al., 2014; Hope et al., 2003). Along environmental gradients, turnover in species can obscure significant shifts in community composition, and linear responses in species richness and other univariate community metrics do not rule out the presence of community thresholds (King and Baker, 2014).

Finally, traditional methods of sampling may not achieve the same results in urban ecosystems as in natural areas, or may change the unit of analysis from the intended unit of analysis to that of the method (e.g. point counts) (Watson, 2003). As a field, we must examine the methods used, why they are used, and how the method used impacts our results.

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# Appendix A

# Vegetation

## A.1 Master set of interview questions

The following questions were used for elite interviews of land owners and landscape maintenance professionals.

- Where do these activities take place?
- How long are landscapers on site?
- What are your typical maintenance activities at this property (weekly, monthly, seasonally)?
  - This question is meant to help guide the following more detailed questions.
- Where on the property do you perform these activities?
  - Examples: lawn, border ornamentals, etc.
- How often do you weed manually?
- Do you uproot/disturb mushrooms when you find them?
- How often do you apply herbicide, and how much? (rough measure e.g. frequent/rarely/never, H/M/L)
  - Same question repeated for fertilizer, fungicide, and insecticide.
- How do you decide when to apply (fertilizer, herbicide, fungicide, insecticide)?

  - Is (fertilizer, herbicide, fungicide, insecticide) at a set rate per month/season?
  - If not, are there criteria used?

- Do you use supplemental irrigation?
  - Is the irrigation system on a timer?
  - Criteria for application if not?

- How often do you apply mulch, what type, and how much?
  - Criteria for application?

## A.2 Full tree species list

| Taxa | Common Name | Origin | Total Abundance | Mean Abundance | Abundance SD |
|---|---|---|---:|---:|---:|
| Acer ginnala | Amur maple | Non-native | 2 | 0.10 | 0.447 |
| Acer macrophyllum | Bigleaf maple | Native | 218 | 10.90 | 17.146 |
| Acer platanoides | Norway maple | Non-native | 100 | 5.00 | 12.074 |
| Acer rubrum | Red maple | Non-native | 132 | 6.60 | 9.725 |
| Acer saccharum | Sugar maple | Non-native | 43 | 2.15 | 6.523 |
| Alnus rubra | Red alder | Native | 29 | 1.45 | 2.305 |
| Arbutus menziesii | Pacific madrone | Native | 19 | 0.95 | 2.685 |
| Betula occidentalis | Red birch | Ambiguous | 3 | 0.15 | 0.671 |
| Betula papyrifera | Paper birch | Native | 7 | 0.35 | 0.745 |
| Betula pendula | Silver birch | Non-native | 3 | 0.15 | 0.489 |
| Carpinus sp. | Hornbeam | Non-native | 3 | 0.15 | 0.671 |
| Cedrus deodara | Deodar cedar | Non-native | 13 | 0.65 | 1.387 |
| Cercidiphyllum japonicum | Katsura | Non-native | 5 | 0.25 | 1.118 |
| Cercis canadensis | Redbud | Non-native | 8 | 0.40 | 1.392 |
| Cupressus nootkatensis | Alaska cedar | Native | 57 | 2.85 | 8.911 |
| Fagus sylvatica gp. | Beech | Non-native | 2 | 0.10 | 0.308 |
| Fraxinus americana | White ash | Non-native | 35 | 1.75 | 6.051 |
| Fraxinus pennsylvanica | Green ash | Non-native | 17 | 0.85 | 3.573 |
| Gleditsia triacanthos | Honey locust | Non-native | 9 | 0.45 | 1.791 |
| Liquidambar styraciflua | Sweetgum | Non-native | 24 | 1.20 | 3.156 |
| Liriodendron tulipifera | Tulip tree | Non-native | 7 | 0.35 | 0.988 |
| Magnolia grandiflora | Southern magnolia | Non-native | 11 | 0.55 | 1.432 |
| Malus sp. | Apple sp. | Non-native | 6 | 0.30 | 0.923 |

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|---|---|---|---|---|---|
| Picea omorika | Weeping Serbian spruce | Non-native | 6 | 0.30 | 1.342 |
| Pinus contorta | Shore pine | Native | 8 | 0.40 | 1.789 |
| Pinus nigra | Black pine | Non-native | 75 | 3.75 | 10.944 |
| Pinus strobus | White pine | Ambiguous | 1 | 0.05 | 0.224 |
| Pinus sylvestris | Scots pine | Non-native | 17 | 0.85 | 2.059 |
| Platanus occidentalis | Flowering plum or cherry | Non-native | 3 | 0.15 | 0.489 |
| Populus nigra | Lombardy poplar | Non-native | 9 | 0.45 | 2.012 |
| Populus tremuloides | Quaking aspen | Ambiguous | 17 | 0.85 | 3.801 |
| Populus trichocarpa | Black cottonwood | Native | 13 | 0.65 | 1.268 |
| Prunus sp. | Flowering plum or cherry | Non-native | 39 | 1.95 | 2.819 |
| Prunus subg. Padus | Choke cherries | Ambiguous | 2 | 0.10 | 0.447 |
| Pseudotsuga menziesii | Douglas fir | Native | 746 | 37.30 | 50.751 |
| Quercus palustris | Pin oak | Non-native | 8 | 0.40 | 1.231 |
| Quercus rubra | Red oak | Non-native | 11 | 0.55 | 2.038 |
| Robinia pseudoacacia | Black locust | Non-native | 3 | 0.15 | 0.671 |
| Sorbus aucuparia | European mountain ash | Non-native | 1 | 0.05 | 0.224 |
| Taxus brevifolia | Pacific yew | Native | 1 | 0.05 | 0.224 |
| Thuja plicata | Western red cedar | Native | 245 | 12.25 | 15.269 |
| Tilia sp. | Linden sp. | Non-native | 1 | 0.05 | 0.224 |
| Tsuga heterophylla | Western hemlock | Native | 5 | 0.25 | 0.716 |
| Ulmus sp. | Elm sp. | Non-native | 4 | 0.20 | 0.894 |
| Unknown Broadleaf 1 | Unknown broadleaf 1 | Ambiguous | 2 | 0.10 | 0.447 |
| Unknown Broadleaf 2 | Unknown broadleaf 2 | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown Broadleaf 3 | Unknown broadleaf 3 | Ambiguous | 1 | 0.05 | 0.224 |

| | | | | | |
|---|---|---|---|---|---|
| Unknown Broadleaf 4 | Unknown broadleaf 4 | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown Broadleaf 5 | Unknown broadleaf 5 | Ambiguous | 2 | 0.10 | 0.447 |
| Unknown Broadleaf 6 | Unknown broadleaf 6 | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown Cedar 1 | Cedar 1 | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown Cedar 2 | Cedar 2 | Ambiguous | 1 | 0.05 | 0.224 |

## A.3 Full shrub species list

| Taxa | Common Name | Origin | Total Abundance | Mean Abundance | Abundance SD |
|---|---|---|---|---|---|
| Abelia grandiflora | Glossy abelia | Non-native | 29 | 1.45 | 6.485 |
| Acer circinatum | Vine maple | Native | 265 | 13.25 | 19.628 |
| Acer palmatum | Japanese maple | Non-native | 17 | 0.85 | 2.183 |
| Amelanchier alnifolia | Saskatoon | Native | 4 | 0.20 | 0.894 |
| Arbutus unedo | Strawberry tree | Non-native | 125 | 6.25 | 17.262 |
| Arctostaphylos sp. | Manzanita | Native | 15 | 0.75 | 3.354 |
| Aucuba japonica | Spotted laurel | Non-native | 7 | 0.35 | 0.988 |
| Berberis thunbergii | Barberry | Non-native | 144 | 7.20 | 21.222 |
| Buxus sp. | Boxwood | Non-native | 65 | 3.25 | 11.548 |
| Calluna vulgaris | Common heather | Non-native | 28 | 1.40 | 5.576 |
| Cistaceae sp. | Rockrose | Ambiguous | 56 | 2.80 | 9.328 |
| Cornus alba gp. | Shrubby dogwood gp. | Ambiguous | 419 | 20.95 | 43.685 |
| Cornus florida gp. | Flowering dogwood gp. | Non-native | 12 | 0.60 | 1.569 |
| Corylus sp. | Hazelnut | Native | 109 | 5.45 | 13.249 |
| Cotoneaster sp. | Cotoneaster | Non-native | 85 | 4.25 | 9.296 |
| Crataegus sp. | Hawthorn | Ambiguous | 11 | 0.55 | 1.146 |
| Cytisus scoparius | Scotch broom | Non-native | 9 | 0.45 | 1.395 |
| Daphne sp. | Daphne | Non-native | 4 | 0.20 | 0.894 |
| Elaeagnus commutata | Silverberry | Native | 31 | 1.55 | 6.932 |
| Enkianthus campanulatus | Enkianthus | Non-native | 2 | 0.10 | 0.447 |
| Erica sp. | Winter heath | Non-native | 16 | 0.80 | 1.609 |
| Escallonia sp. | Escallonia | Non-native | 40 | 2.00 | 5.301 |

| | | | | | |
|---|---|---|---|---|---|
| Euonymus alatus | Winged euonymus | Non-native | 127 | 6.35 | 13.620 |
| Euonymus japonicus | Japanese spindle | Non-native | 76 | 3.80 | 5.197 |
| Euphorbia sp. | Euphorbia | Non-native | 56 | 2.80 | 5.662 |
| Forsythia sp. | Forsythia | Non-native | 76 | 3.80 | 14.059 |
| Gardenia sp. | Gardenia | Non-native | 3 | 0.15 | 0.671 |
| Gaultheria shallon | Salal | Native | 1267 | 63.35 | 115.281 |
| Hebe sp. | Hebe | Non-native | 31 | 1.55 | 5.094 |
| Hibiscus syriacus | Rose of Sharon (hibiscus) | Non-native | 2 | 0.10 | 0.447 |
| Holodiscus discolor | Oceanspray | Native | 7 | 0.35 | 1.565 |
| Hydrangea sp. | Hydrangea | Non-native | 15 | 0.75 | 1.860 |
| Hypericum calycinum | St. John’s wort | Non-native | 71 | 3.55 | 8.894 |
| Ilex aquifolium gp. | Common holly group | Ambiguous | 30 | 1.50 | 2.947 |
| Ilex crenata | Japanese holly | Non-native | 138 | 6.90 | 10.711 |
| Kalmia latifolia | Mountain laurel | Non-native | 2 | 0.10 | 0.447 |
| Lavandula sp. | Lavender | Non-native | 46 | 2.30 | 9.592 |
| Leucothoe fontanesiana | Leucothoe | Non-native | 8 | 0.40 | 1.273 |
| Leycesteria formosa | Himalayan honeysuckle | Non-native | 17 | 0.85 | 3.801 |
| Lonicera pileata | Privet honeysuckle | Non-native | 136 | 6.80 | 30.411 |
| Lonicera sempervirens gp. | Trumpet honeysuckle | Non-native | 9 | 0.45 | 2.012 |
| Mahonia sp. | Mahonia | Ambiguous | 1007 | 50.35 | 93.443 |
| Nandina domestica | Heavenly bamboo | Non-native | 168 | 8.40 | 23.359 |
| Oemleria cerasiformis | Indian plum | Native | 146 | 7.30 | 11.721 |

| | | | | | |
|---|---|---|---|---|---|
| Ornamental conifer | Ornamental conifer | Ambiguous | 177 | 8.85 | 11.431 |
| Osmanthus burkwoodii | Burkwood osmanthus | Non-native | 76 | 3.80 | 14.348 |
| Philadelphus lewisii | Mock orange | Native | 2 | 0.10 | 0.447 |
| Photinia fraseri | Fraser's Photinia | Non-native | 66 | 3.30 | 6.131 |
| Physocarpus opulifolious | Ninebark | Non-native | 9 | 0.45 | 2.012 |
| Pieris japonica | Japanese pieris | Non-native | 34 | 1.70 | 3.310 |
| Potentilla fruticosa | White potentilla | Native | 19 | 0.95 | 4.249 |
| Prunus laurocerasus | Cherry laurel | Non-native | 101 | 5.05 | 9.344 |
| Prunus laurocerasus var. zabeliana | Zabel laurel | Non-native | 581 | 29.05 | 37.841 |
| Rahpiolepsis indica | Indian hawthorne | Non-native | 4 | 0.20 | 0.894 |
| Rhododendron sp. | Rhododendron | Ambiguous | 612 | 30.60 | 21.507 |
| Rhus sp. | Sumac | Ambiguous | 25 | 1.25 | 4.115 |
| Ribes sanguineum | Red flowering currant | Native | 143 | 7.15 | 14.057 |
| Rosa sp. | Domestic rose | Ambiguous | 46 | 2.30 | 6.760 |
| Rosmarinus officinalis | Rosemary | Non-native | 1 | 0.05 | 0.224 |
| Rubus armeniacus | Himalayan blackberry | Non-native | 119 | 5.95 | 10.655 |
| Rubus laciniatus | Evergreen blackberry | Non-native | 25 | 1.25 | 5.590 |
| Rubus spectabilis | Salmonberry | Native | 48 | 2.40 | 6.954 |
| Sambucus sp. | Elderberry | Ambiguous | 3 | 0.15 | 0.671 |
| Sarcococca confusa | Sweet box | Non-native | 69 | 3.45 | 11.528 |

| | | | | | |
|---|---|---|---|---|---|
| Spiraea japonica gp. | Spiraea japonica gp. | Non-native | 57 | 2.85 | 11.412 |
| Spiraea nipponica | Japanese spirea | Non-native | 59 | 2.95 | 11.651 |
| Styrax japonicus | Japanese snowball | Non-native | 11 | 0.55 | 1.317 |
| Unknown L gp. | Unknown L gp. | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown N gp. | Unknown N gp. | Ambiguous | 5 | 0.25 | 1.118 |
| Unknown S gp. | Unknown S gp. | Ambiguous | 1 | 0.05 | 0.224 |
| Vaccinium cyanococcus gp. | Blueberry | Native | 5 | 0.25 | 1.118 |
| Symphoricarpos sp. | Snowberry | Native | 148 | 7.40 | 14.848 |
| Syringa vulgaris | Lilac | Non-native | 2 | 0.10 | 0.308 |
| Thuja occidentalis | Arborvitae | Non-native | 31 | 1.55 | 4.006 |
| Unknown B gp. | Unknown B gp. | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown C gp. | Unknown C gp. | Ambiguous | 2 | 0.10 | 0.447 |
| Unknown F gp. | Unknown F gp. | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown G gp. | Unknown G gp. | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown J gp. | Unknown J gp. | Ambiguous | 1 | 0.05 | 0.224 |
| Unknown K gp. | Unknown K gp. | Ambiguous | 1 | 0.05 | 0.224 |

## A.4 Observed sample and population distributions

My sampling design was stratified by assigned vegetation class and bounded by two independent variables—parcel area and percent impervious surface within 500 m of the parcel. Therefore:

1. vegetation class of the sample should be more evenly distributed than the vegetation class of the population (Figure A.1);
2. the parcel area of the sample should be both a subset of the area of the population have a larger median (bounded 25-85% of size distribution; Figure A.2);
3. the percent impervious surface of the sample should be from a narrower distribution but centered around the same mean as the percent impervious surface of the population (bounded 15-85% of distribution; Figure A.2); and
4. for all other independent variables describing the parcels, the sample should reflect the distribution of the broader population (Table A.3).

Overall, my disproportionate stratified random sample achieved good coverage of the vegetation gradient on office developments. Except for site area, which is larger for the sample than the population, other independent variables have similar means for sample and population. However, the small sample size (20 sites) results in not sampling across some socio-economic gradients.

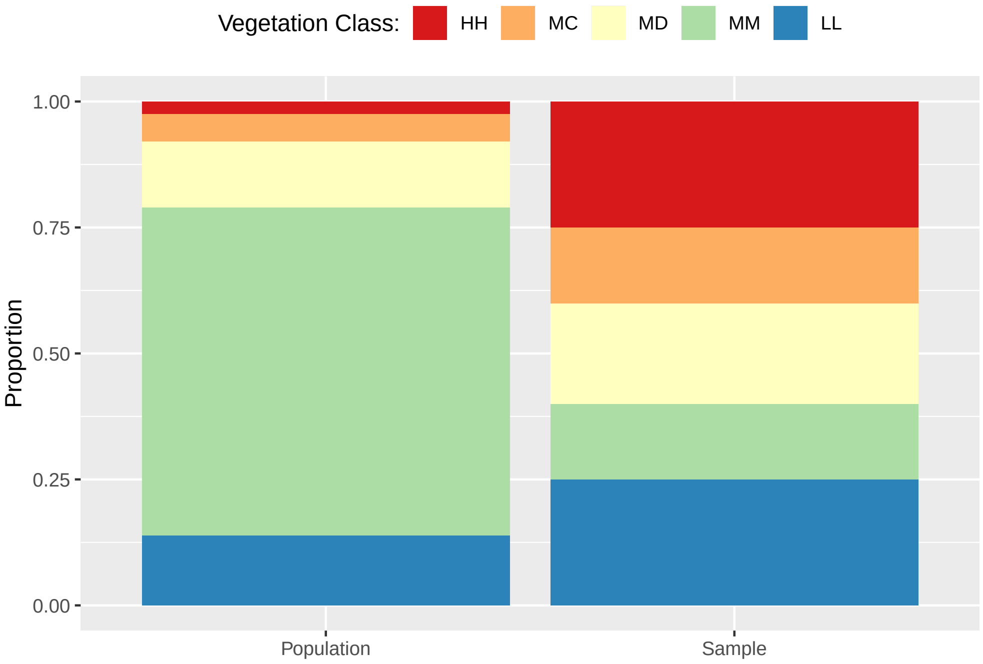

Figure A.1: Point 1: Vegetation class of the sample is more evenly distributed than that of the population.

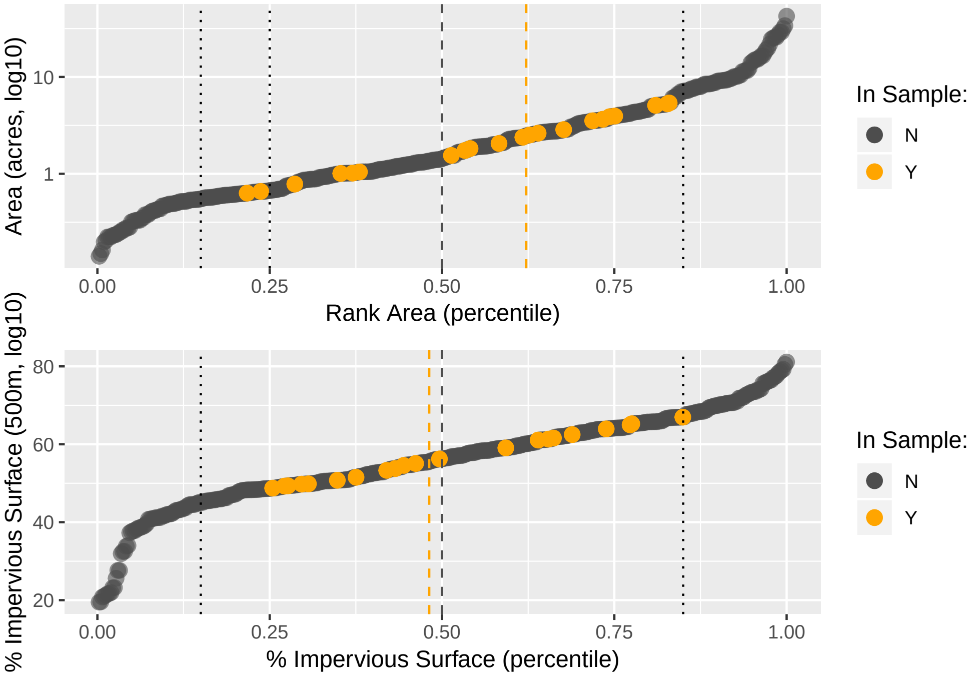

Figure A.2: (L) Point 2: Parcel area of the sample is appropriately bounded and has a larger median than that of the population. (R) Point 3: Surrounding % impervious surface of the sample is appropriately bounded and has approximately the same median as that of the population (500 m mean value buffered on parcel outline).

Table A.3: Point 4: Summary statistics for independent variables for both the population of business parks in Redmond and Bellevue and the sample of sites studied. Area (acres) and year built (transformed to building age) are site-scale covariates, while the others are neighborhood-scale covariates. Sites were selected based on area and percent impervious. Median income ($) and % foreign born are included as they were significant in residential research and to see if commercial developments follow similar patterns or are influenced by surrounding residential property.

| Metric | Minimum | Maximum | Mean | S.D. | Median |
|---|---|---|---|---|---|
| Sample: Area (acres) | 0.63 | 5.39 | 2.57 | 1.58 | 2.45 |
| Population: Area (acres) | 0.03 | 42.51 | 3.21 | 5.17 | 1.20 |
| Sample: Percent Impervious w/in 500m | 48.75 | 66.96 | 56.76 | 6.29 | 55.66 |
| Population: Percent Impervious w/in 500m | 19.33 | 81.11 | 56.31 | 12.07 | 57.78 |
| Sample: Year Built | 1975 | 2008 | 1984.92 | 9.77 | 1982.00 |
| Population: Year Built | 1911 | 2013 | 1981.85 | 14.09 | 1983.00 |
| Sample: Median Income ($) | 42368 | 134643 | 80477.50 | 22179.18 | 73754.00 |
| Population: Median Income ($) | 38804 | 194107 | 81808.41 | 24175.64 | 80750.00 |
| Sample: Percent Foreign-Born | 0.15 | 0.86 | 0.41 | 0.18 | 0.37 |
| Population: Percent Foreign-Born | 0.15 | 0.86 | 0.39 | 0.16 | 0.40 |

## A.5 Shrub and tree diversity indicies

I found variation in the species richness (number of species per site) and evenness ( $H'/log_{10}(richness)$ ) between sites. Effective species richness is higher and more variable for shrubs than trees, and evenness is generally higher and less variable for shrubs than trees. This suggests that shrub species are usually planted evenly at business developments, though how many species are planted varies widely. There there are consistently only a few tree species at business developments, but the sites vary greatly in how evenly these species are distributed.

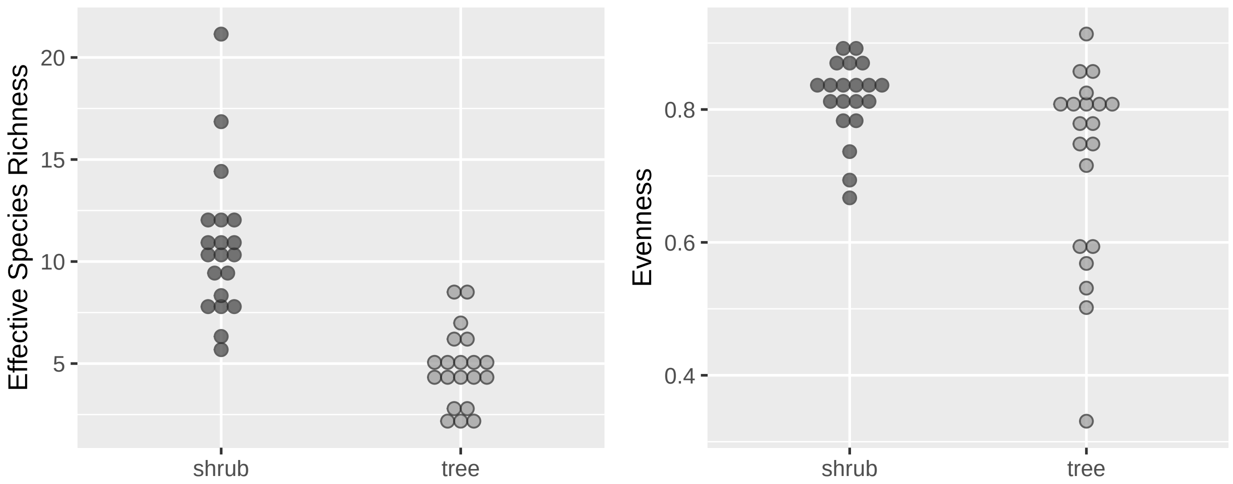

Figure A.3: Comparison of shrub and tree diversity indices.

This pattern may be related to the preservation of existing native species during development. Sites with low tree evenness are more dominated by native conifers (L; both planted and preserved through development). The three key species are western red cedar ( *Thuja plicata* ), Douglas fir ( *Pseudotsuga menziesii* ), and western hemlock ( *Tsuga heterophylla* ). However, the number of native conifers is not related to the site's tree species richness, suggesting that even sites dominated by native conifers are generally planted with multiple ornamental tree species (R).

For these graphs and those that follow, note that the green line is a linear model estimation with the 95% confidence interval shown in gray. Where this confidence interval includes the horizontal line (constant y), the $H_0 : slope = 0$ model cannot be rejected.

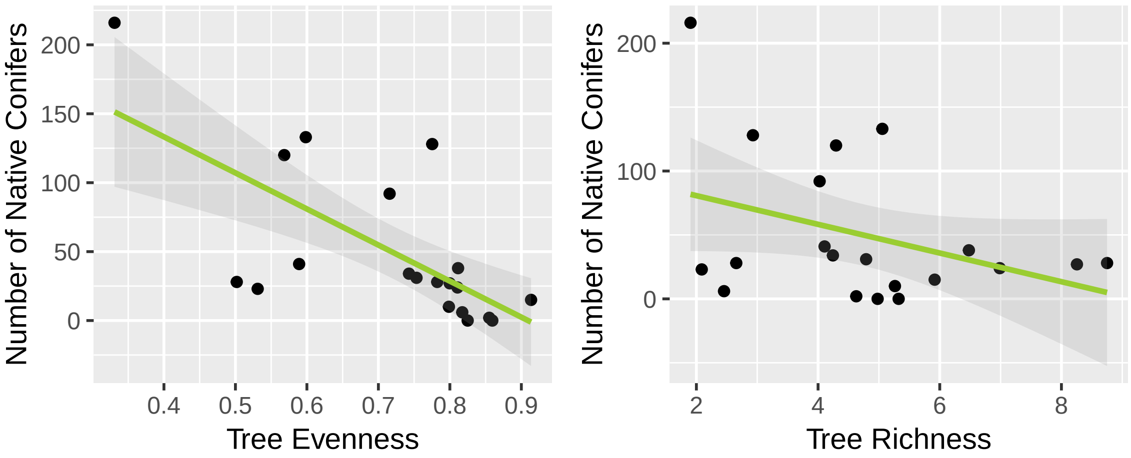

Figure A.4: Number of native conifers plotted with office development tree evenness and tree species richness

For shrubs, there is no significant relationship between the abundance of native conifers and shrub evenness or richness. These one-dimensional indices suggest that shrub landscaping is independent of the number of native conifers—but note that they say nothing about the makeup of the shrub community.

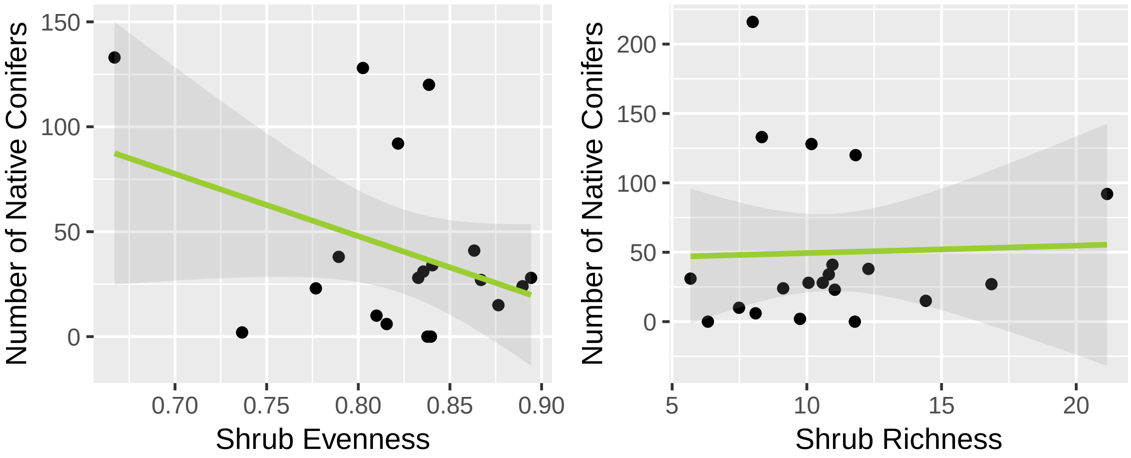

Figure A.5: Number of native conifers plotted with office development shrub evenness and richness. Note that I removed one outlier site with extremely low shrub evenness due to high salal abundance to make this pattern more clear; it does not change the result.

Within sites, shrub species evenness and richness and tree species evenness and richness are not related. Additionally, there is no relationship between shrub and tree effective species richness, or tree and shrub evenness.

## A.6 Comparing assigned vegetation classes

I used ANOVA to compare vegetation classes assigned during site selection with observed tree and shrub data (density of large native conifers and shrub species richness) using the aov {stats} function. For native tree density, I set up ANOVA contrasts to test the difference between all vegetation classes, between pooled LL/MM/MD and MC/HH classes, between LL/MM/MD and between MC/HH[1]. For effective shrub species richness, I set up ANOVA contrasts between pooled LL/MM/MC and MD/HH classes and within classes.

As expected, conifer density on 'High' and 'Medium Canopy' sites is significantly greater than 'Low', 'Medium', and 'Medium Diverse' sites (contrast $\Pr(>|t|) = 0.005$). The two outliers in the 'Medium Diverse' and 'Low' categories resulted from initial classification errors and highlight the difficulty of rapid classification in urban areas with uncertain boundaries[2].

Shrub species richness was more similar across sites than expected, and no significant differences between groups were detected. With few exceptions, raw shrub species richness and effective species richness ranged between 10-25 species and 7-13 species, respectively (effective richness defined as exp(H'); Jost, 2006). Effective shrub species richness on 'High' and 'Medium Diverse' sites was not statistically different than 'Low', 'Medium', and 'Medium Canopy' sites (contrast $\Pr(>|t|) = 0.292$; Figure A.6). While the range of observed shrub richness suggest that the sites I surveyed have a broad enough range to draw conclusions about shrubs on office developments, there are few replicates with very high levels of shrub richness.

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[1] I used contrasts instead of Tukey HSD because it is appropriate for a priori comparisons and has more power.

[2] The notable exception in the 'Medium Diverse' category had an undeveloped woodlot at the back of the property that was not easily visible during classification; the native conifers planted at the 'Low' site exception were ambiguously located at the boundary edge of the property. In hindsight, the LL outlier should have been classified MM and the MD outlier should have been classified as HH

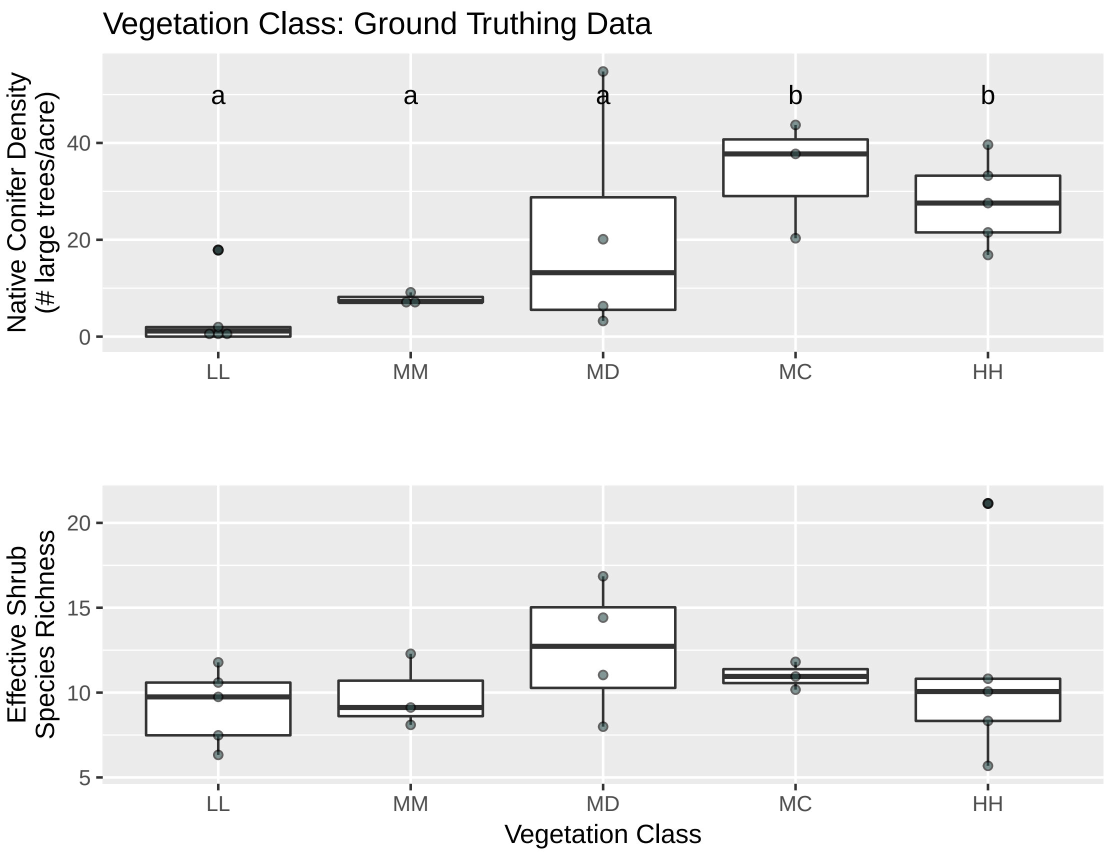


Figure A.6: Comparison of vegetation classes assigned during site selection. (Top): As expected, native conifer density is significantly higher on Medium Canopy and High vegetation class sites. (Bottom): Contrary to expectations, effective shrub species richness was not significantly different across vegetation classes.

## A.7 Vegetation rank abundance

Figure A.4 shows the ten most abundant tree and shrub species for community groups identified using flexible-beta cluster analysis. Both native tree and shrub community typologies are dominated by native species like western red cedar, while non-native ornamentals largely from the eastern United States and Asia dominate the ornamental lists. Note that some species span both lists. For example, Douglas-fir are widely planted on both native and ornamental tree community typologies, but the relative abundance is greatly reduced in ornamental tree communities.

Table A.4: Rank abundance of tree and shrub species for each community group identified by flexible-beta analysis.

| Rank | Native Tree Group | Ornamental Tree Group | Native Shrub Group | Ornamental Shrub Group |
|---|---|---|---|---|
| 1 | douglas fir (645) | douglas fir (101) | gaultheria shallon (1177) | prunus laurocerasus zabeliana (486) |
| 2 | western red cedar (224) | red maple (98) | mahonia sp (941) | rhododendron sp (270) |
| 3 | big leaf maple (213) | norway maple (94) | rhododendron sp (342) | cornus alba gp (211) |
| 4 | red maple (34) | black pine (72) | acer circinatum (219) | lonicera pileata (136) |
| 5 | red alder (24) | alaska cedar (49) | cornus alba gp (208) | viburnum davidii (123) |
| 6 | pacific madrone (19) | sugar maple (43) | vaccinium ovatum (201) | berberis thunbergii (118) |
| 7 | quaking aspen (17) | white ash (35) | viburnum davidii (155) | ilex crenata (91) |
| 8 | sweetgum (13) | prunus sp (30) | symphoricarpos sp (147) | gaultheria shallon (90) |
| 9 | prunus sp (9) | western red cedar (21) | ribes sanguineum (137) | ornamental conifer (88) |
| 10 | alaska cedar (8) | green ash (17) | arbutus unedo (124) | osmanthus burkwoodii (74) |

## A.8 PERMANOVA simple multivariate regression results

Table A.5 shows all simple multivariate model results for shrub community composition, expressed as density (shrubs/acre).

Table A.5: Multivariate simple PERMANOVA model results for the shrub community, expressed as density (shrubs/acre).

| | Variation Explained | Pseudo-F | p-value (Location) | p-value (Dispersion) |
|---|---|---|---|---|
| Shrub Community Cluster | 0.215 | 4.943 | 0.000 | 0.506 |
| Vegetation Class | 0.337 | 1.904 | 0.001 | 0.971 |
| Site Area (acres) | 0.081 | 1.583 | 0.084 | NA |
| Building Age (years) | 0.078 | 1.523 | 0.096 | NA |
| Building Quality | 0.179 | 1.162 | 0.228 | 0.396 |
| Mean Impervious within 500 m (%) | 0.045 | 0.858 | 0.588 | NA |
| Town (Redmond/Bellevue) | 0.060 | 1.149 | 0.280 | 0.483 |
| Assessed Land Value per Acre | 0.061 | 1.172 | 0.270 | NA |
| Median Household Income (USD) | 0.068 | 1.315 | 0.178 | NA |
| Foreign Born (%) | 0.078 | 1.520 | 0.097 | NA |
| Short and Medium Vegetation within 500 m (%) | 0.059 | 1.123 | 0.304 | NA |
| Tall Vegetation within 500 m (%) | 0.062 | 1.188 | 0.254 | NA |
| Dead Wood Abundance | 0.077 | 1.503 | 0.098 | NA |
| Median Douglas Fir Height (m) | 0.155 | 3.291 | 0.000 | NA |
| Stands Predate Development | 0.116 | 2.351 | 0.010 | 0.699 |
| Tree Community Cluster | 0.147 | 3.104 | 0.002 | 0.701 |
| Native Conifer Density | 0.142 | 2.980 | 0.001 | NA |
| Fertilizer (Y/N) | 0.080 | 0.739 | 0.857 | 0.011 |
| Herbicide (Y/N) | 0.109 | 1.035 | 0.401 | 0.008 |
| Irrigation (Y/N) | 0.107 | 1.023 | 0.417 | 0.000 |
| Mulch (Y/N) | 0.064 | 1.226 | 0.239 | 0.017 |
| Mushroom (Y/N) | 0.095 | 0.895 | 0.600 | 0.727 |

# Appendix B

# Bird

## B.1 All bird species observed

Table B.1 lists all birds observed during fieldwork in winters 2014-2015 and 2015-2016.

Table B.1: All observed bird species.

| Common Name | Scientific Name | Num Sites Seen | Median Incidence | Num Sites Seen Foraging | Median Foraging Incidence |
|---|---|---|---|---|---|
| American Crow | Corvus brachyrhynchos | 20 | 0.75 | 19 | 0.4375 |
| American Goldfinch | Spinus tristis | 1 | 0 | 1 | 0 |
| American Robin | Turdus migratorius | 20 | 0.5 | 20 | 0.25 |
| Anna's Hummingbird | Calypte anna | 20 | 0.625 | 15 | 0.125 |
| Audubon's Warbler | Dendroica coronata auduboni | 6 | 0 | 6 | 0 |
| Band-tailed Pigeon | Patagioenas fasciata | 2 | 0 | 0 | 0 |
| Bewick's Wren | Thryomanes bewickii | 18 | 0.375 | 16 | 0.25 |
| Black-capped Chickadee | Poecile atricapillus | 20 | 0.6875 | 20 | 0.5625 |
| Brown Creeper | Certhia americana | 11 | 0.125 | 11 | 0.125 |
| Bushtit | Psaltriparus minimus | 6 | 0 | 6 | 0 |
| Chestnut-backed Chickadee | Poecile rufescens | 19 | 0.625 | 19 | 0.5625 |
| Common Raven | Corvus corax | 1 | 0 | 0 | 0 |
| Dark-eyed Junco | Junco hyemalis | 20 | 0.875 | 20 | 0.75 |
| Downy Woodpecker | Dryobates pubescens | 1 | 0 | 1 | 0 |
| European Starling | Sturnus vulgaris | 11 | 0.125 | 4 | 0 |
| Fox Sparrow | Passerella iliaca | 2 | 0 | 1 | 0 |
| Golden-crowned Kinglet | Regulus satrapa | 20 | 0.75 | 20 | 0.625 |
| House Finch | Carpodacus mexicanus | 7 | 0 | 3 | 0 |
| House Sparrow | Passer domesticus | 1 | 0 | 1 | 0 |
| Hutton's Vireo | Vireo huttoni | 1 | 0 | 0 | 0 |
| Killdeer | Charadrius vociferus | 1 | 0 | 0 | 0 |
| No Birds | no birds | 8 | 0 | 0 | 0 |
| Northern Flicker | Colaptes auratus | 18 | 0.25 | 7 | 0 |
| Pacific Wren | Troglodytes pacificus | 7 | 0 | 7 | 0 |
| Pileated Woodpecker | Dryocopus pileatus | 2 | 0 | 0 | 0 |
| Pine Siskin | Carduelis pinus | 12 | 0.125 | 9 | 0 |
| Purple Finch | Carpodacus purpureus | 4 | 0 | 3 | 0 |
| Red-breasted Nuthatch | Sitta canadensis | 16 | 0.3125 | 13 | 0.125 |
| Red-breasted Sapsucker | Sphyrapicus ruber | 12 | 0.125 | 11 | 0.125 |
| Red Crossbill | Loxia curvirostra | 7 | 0 | 4 | 0 |
| Rock Pigeon | Columba livia | 1 | 0 | 1 | 0 |
| Ruby-crowned Kinglet | Regulus calendula | 17 | 0.4375 | 17 | 0.375 |
| Song Sparrow | Melospiza melodia | 15 | 0.3125 | 14 | 0.125 |
| Spotted Towhee | Pipilo maculatus | 16 | 0.25 | 15 | 0.125 |
| Stellers Jay | Cyanocitta stelleri | 10 | 0.0625 | 5 | 0 |
| Townsend's Warbler | Dendroica townsendi | 5 | 0 | 5 | 0 |
| Varied Thrush | Ixoreus naevius | 8 | 0 | 7 | 0 |

## B.2 Explaining variation in effective species richness

All univariate PERMANOVA model results for bird effective species richness. Detection variables, including variables median air temperature through total precipitation in Table B.2 were tested in simple models. All other variables were tested with the % of overcast visits as the control variable.

Table B.2: Univariate model results for bird effective species richness. Detection variables are tested alone; the percentage of overcast visits is used as a control variable.

| | Variation Explained | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Median Average Air Temperature (F) | 0.001 | 0.014 | 0.907 | 23.34 |
| Overcast Visits (%; Control Var) | 0.303 | 7.835 | 0.013 | 16.13 |
| Drizzle Visits (%) | 0.082 | 1.600 | 0.220 | 21.65 |
| Fog Visits (%) | 0.043 | 0.803 | 0.385 | 22.48 |
| Median Wind Gusts (MPH) | 0.044 | 0.830 | 0.378 | 22.45 |
| Loud Noise Visits (%) | 0.091 | 1.796 | 0.195 | 21.45 |
| Median Solar Radiation (W/m^2) | 0.102 | 2.035 | 0.173 | 21.21 |
| Median Wind Speed (MPH) | 0.011 | 0.200 | 0.671 | 23.14 |
| Total Precipitation (in) | 0.066 | 1.280 | 0.290 | 21.98 |
| Site Area (acres) | 0.036 | 0.926 | 0.351 | 17.86 |
| Building Age (years) | 0.000 | 0.001 | 0.974 | 18.92 |
| Building Quality | 0.125 | 1.088 | 0.383 | 21.77 |
| Mean Impervious within 500m (%) | 0.007 | 0.164 | 0.689 | 18.73 |
| Major Intersections within 500m | 0.090 | 2.513 | 0.129 | 16.17 |
| Town (Redmond/Bellevue) | 0.018 | 0.451 | 0.508 | 18.40 |
| Assessed Value per Acre | 0.007 | 0.166 | 0.692 | 18.73 |
| Median Household Income (USD) | 0.015 | 0.380 | 0.548 | 18.48 |
| Foreign Born (%) | 0.007 | 0.175 | 0.681 | 18.72 |
| Short and Medium Vegetation within 500m (%) | 0.075 | 2.049 | 0.172 | 16.65 |
| Tall Vegetation within 500m (%) | 0.009 | 0.218 | 0.646 | 18.67 |
| Cleanup (Y/N) | 0.039 | 1.001 | 0.317 | 17.78 |
| Dead Wood Abundance | 0.109 | 3.160 | 0.091 | 15.51 |
| Fertilizer (Y/N) | 0.019 | 0.225 | 0.811 | 21.54 |
| Median Douglas Fir Height (m) | 0.426 | 26.790 | 0.000 | 0.00 |
| Herbicide (Y/N) | 0.007 | 0.076 | 0.927 | 21.90 |
| On Site Impervious (%) | 0.201 | 6.890 | 0.018 | 12.12 |
| Irrigation (Y/N) | 0.083 | 1.088 | 0.382 | 19.54 |
| Mulch (Y/N) | 0.039 | 0.999 | 0.338 | 17.78 |
| Mushroom (Y/N) | 0.185 | 2.890 | 0.086 | 15.92 |
| Native Shrub Effective Richness | 0.216 | 7.620 | 0.014 | 11.52 |
| Native Shrub Density | 0.205 | 7.083 | 0.018 | 11.96 |
| Stand Predating Development | 0.327 | 15.032 | 0.002 | 6.25 |
| Native Conifer Density | 0.225 | 8.096 | 0.012 | 11.13 |
| Shrub Cluster Group | 0.179 | 5.875 | 0.029 | 12.99 |
| Tree Cluster Group | 0.247 | 9.364 | 0.009 | 10.15 |
| Vegetation Class | 0.274 | 2.263 | 0.113 | 19.91 |

## B.3 Explaining variation in bird and foraging bird community composition

Table B.3: Multivariate simple PERMANOVA model results for the entire bird community, expressed as incidence.

| | Variation Explained | Pseudo-F | Location p-value | Dispersion p-value |
|---|---|---|---|---|
| Median Average Air Temperature (F) | 0.038 | 0.708 | 0.636 | NA |
| Overcast Visits (%) | 0.126 | 2.604 | 0.033 | NA |
| Drizzle Visits (%) | 0.064 | 1.222 | 0.252 | NA |
| Fog Visits (%) | 0.043 | 0.805 | 0.537 | NA |
| Median Wind Gusts (MPH) | 0.051 | 0.958 | 0.416 | NA |
| Loud Noise Visits (%) | 0.070 | 1.353 | 0.202 | NA |
| Median Solar Radiation (W/m^2) | 0.064 | 1.228 | 0.255 | NA |
| Median Wind Speed (MPH) | 0.027 | 0.499 | 0.859 | NA |
| Total Precipitation (in) | 0.049 | 0.919 | 0.477 | NA |
| Site Area (acres) | 0.079 | 1.680 | 0.123 | NA |
| Building Age (years) | 0.044 | 0.895 | 0.461 | NA |
| Building Quality | 0.126 | 0.839 | 0.627 | 0.380 |
| Mean Impervious within 500 m (%) | 0.037 | 0.746 | 0.592 | NA |
| Major Intersections within 500 m | 0.062 | 1.303 | 0.233 | NA |
| Town (Redmond/Bellevue) | 0.048 | 0.984 | 0.388 | 0.691 |
| Assessed Land Value per Acre | 0.056 | 1.155 | 0.293 | NA |
| Median Household Income (USD) | 0.038 | 0.768 | 0.574 | NA |
| Foreign Born (%) | 0.052 | 1.086 | 0.324 | NA |
| Short and Medium Vegetation within 500 m (%) | 0.077 | 1.635 | 0.131 | NA |
| Tall Vegetation within 500m (%) | 0.044 | 0.900 | 0.451 | NA |
| Cleanup (Y/N) | 0.036 | 0.730 | 0.649 | 0.001 |
| Dead Wood Abundance | 0.120 | 2.697 | 0.025 | NA |
| Fertilizer (Y/N) | 0.057 | 0.561 | 0.897 | 0.003 |
| Median Douglas Fir Height (m) | 0.244 | 6.572 | 0.000 | NA |
| Herbicide (Y/N) | 0.054 | 0.525 | 0.923 | 0.268 |
| On Site Impervious (%) | 0.185 | 4.554 | 0.002 | NA |
| Irrigation (Y/N) | 0.071 | 0.712 | 0.758 | 0.000 |
| Mulch (Y/N) | 0.049 | 1.001 | 0.392 | 0.008 |
| Mushroom (Y/N) | 0.148 | 1.628 | 0.106 | 0.906 |
| Native Shrub Effective Richness | 0.156 | 3.684 | 0.008 | NA |
| Native Shrub Density | 0.113 | 2.523 | 0.038 | NA |
| Stands Predate Development | 0.174 | 4.240 | 0.004 | 0.589 |
| Native Conifer Density | 0.185 | 4.572 | 0.002 | NA |
| Shrub Cluster Group | 0.089 | 1.929 | 0.085 | 0.554 |
| Tree Cluster Group | 0.155 | 3.653 | 0.008 | 0.528 |
| Vegetation Class | 0.267 | 1.542 | 0.092 | 0.273 |

Multivariate PERMANOVA model results for foraging bird community. Detection variables are tested in simple models, while overcast visits (%) is used as a control variable in non-detection variable models.

Table B.4: Multivariate simple PERMANOVA model results for the foraging bird community.

| | Variation Explained | Pseudo-F | Location p-value | Dispersion p-value |
|---|---|---|---|---|
| Median Average Air Temperature (F) | 0.049 | 0.935 | 0.433 | NA |
| Overcast Visits (%) | 0.132 | 2.728 | 0.029 | NA |
| Drizzle Visits (%) | 0.076 | 1.488 | 0.170 | NA |
| Fog Visits (%) | 0.047 | 0.889 | 0.468 | NA |
| Median Wind Gusts (MPH) | 0.059 | 1.131 | 0.308 | NA |
| Loud Noise Visits (%) | 0.037 | 0.686 | 0.654 | NA |
| Median Solar Radiation (W/m^2) | 0.084 | 1.661 | 0.128 | NA |
| Median Wind Speed (MPH) | 0.034 | 0.631 | 0.732 | NA |
| Total Precipitation (in) | 0.058 | 1.118 | 0.341 | NA |
| Site Area (acres) | 0.070 | 1.495 | 0.167 | NA |
| Building Age (years) | 0.034 | 0.696 | 0.654 | NA |
| Building Quality | 0.135 | 0.918 | 0.533 | 0.492 |
| Assessed Land Value per Acre | 0.062 | 1.301 | 0.228 | NA |
| Mean Impervious within 500 m (%) | 0.064 | 1.341 | 0.211 | NA |
| Major Intersections within 500 m | 0.050 | 1.041 | 0.360 | 0.890 |
| Town (Redmond/Bellevue) | 0.049 | 1.026 | 0.367 | NA |
| Median Household Income (USD) | 0.026 | 0.516 | 0.831 | NA |
| Foreign Born (%) | 0.051 | 1.068 | 0.342 | NA |
| Short and Medium Vegetation within 500 m (%) | 0.095 | 2.084 | 0.068 | NA |
| Tall Vegetation within 500 m (%) | 0.061 | 1.292 | 0.233 | NA |
| Cleanup (Y/N) | 0.043 | 0.876 | 0.556 | 0.000 |
| Dead Wood Abundance | 0.108 | 2.423 | 0.038 | NA |
| Fertilizer (Y/N) | 0.053 | 0.523 | 0.926 | 0.005 |
| Median Douglas Fir Height (m) | 0.235 | 6.316 | 0.000 | NA |
| Herbicide (Y/N) | 0.048 | 0.470 | 0.950 | 0.413 |
| On Site Impervious (%) | 0.146 | 3.444 | 0.011 | NA |
| Irrigation (Y/N) | 0.080 | 0.808 | 0.668 | 0.000 |
| Mulch (Y/N) | 0.043 | 0.877 | 0.491 | 0.015 |
| Mushroom (Y/N) | 0.169 | 1.928 | 0.057 | 0.694 |
| Native Shrub Effective Richness | 0.165 | 3.984 | 0.005 | NA |
| Native Shrub Density | 0.106 | 2.370 | 0.046 | NA |
| Stands Predate Development | 0.174 | 4.260 | 0.004 | 0.484 |
| Native Conifer Density | 0.182 | 4.505 | 0.002 | NA |
| Shrub Community Cluster | 0.098 | 2.162 | 0.063 | 0.664 |
| Tree Community Cluster | 0.165 | 3.999 | 0.006 | 0.310 |
| Vegetation Class | 0.280 | 1.663 | 0.062 | 0.667 |

## B.4 NMDS visualizations

### B.4.1 All birds

NMDS was used to plot the gradation of community pattern with the variables identified as significant using PERMANOVA (NMDS with k = 2, stress = 0.112, solution reached after 2022 tries). Median Douglas-fir height is strongly correlated with the first axis, while native conifer density, % impervious surface on site, and presence of stands predating development appear correlated with both axes (Figure B.1).

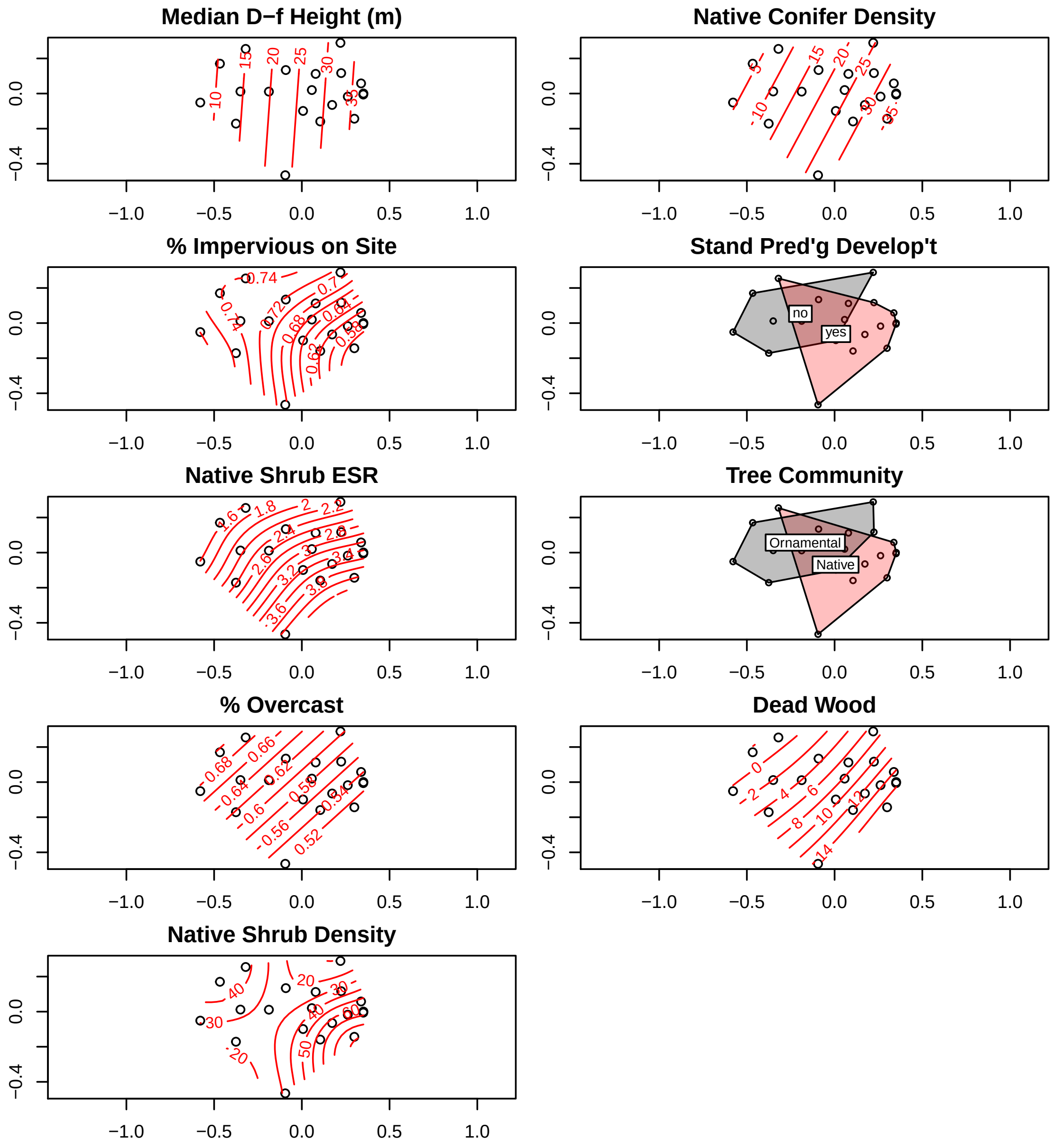
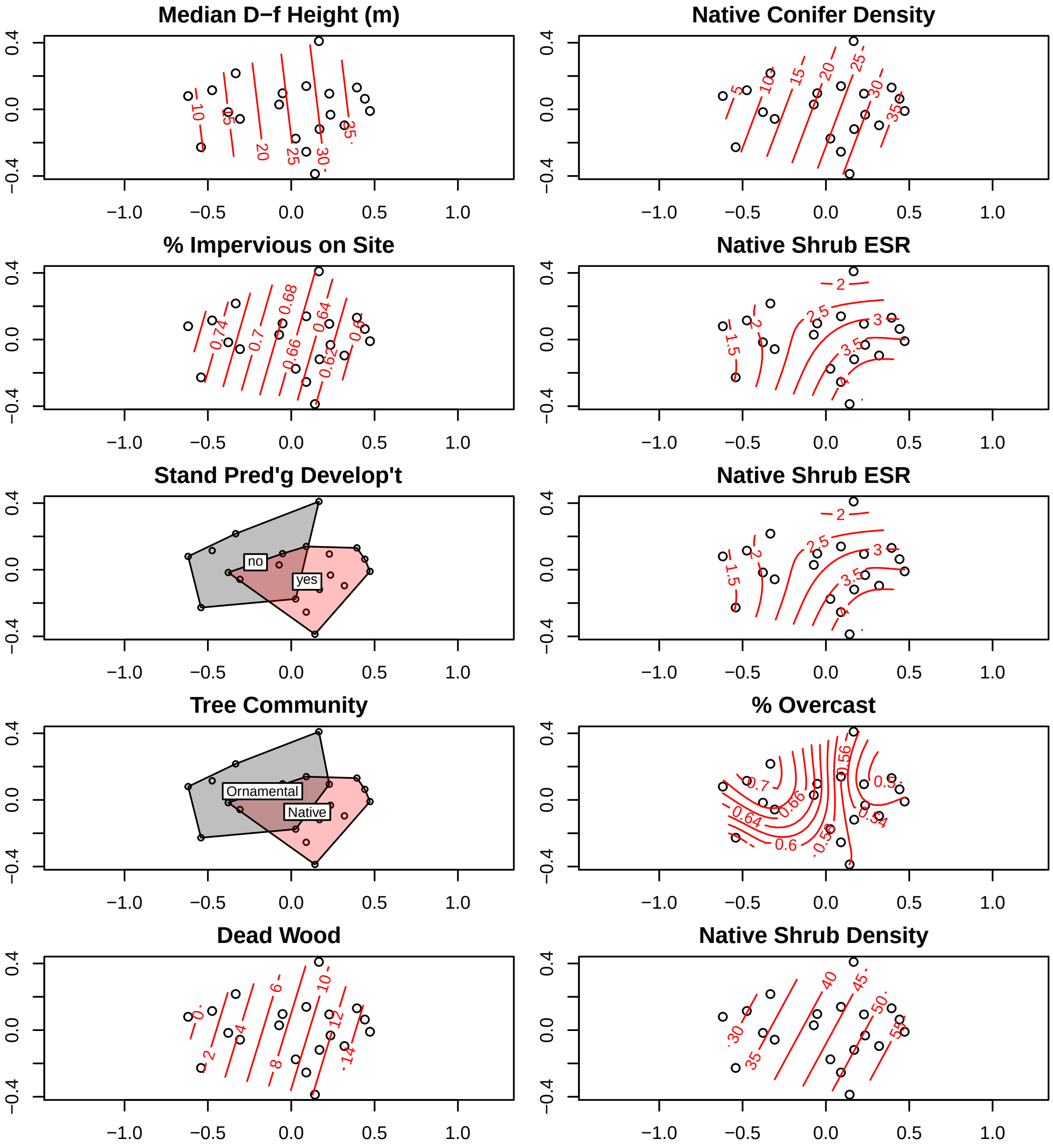


Figure B.1: NMDS of bird community composition on office developments with oridination surfaces for median Douglas-fir height, native conifer density, percent impervious surface on site, and stands predating development. Variables found significant in PERMANOVA analysis.

## B.4.2 Foraging birds

NMDS was also used to plot the gradation pattern of foraging bird community with the variables identified as significant using PERMANOVA (NMDS with k = 2, stress = 0.132, solution reached after 2022 tries). Median Douglas-fir height, native conifer density, and % impervious on site are all correlated with the first axis, while the presence of stands predating development is associated with both axes (Figure B.2).


Median D−f Height (m)

Native Conifer Density

% Impervious on Site

Native Shrub ESR

Stand Pred'g Develop't

Native Shrub ESR

Tree Community

% Overcast

Dead Wood

Native Shrub Density

Figure B.2: NMDS of foraging bird community composition on office developments with oridination surfaces for median Douglas-fir height, native conifer density, percent impervious surface on site, native shrub effective species richness, and stands predating development. Variables found significant in PERMANOVA analysis.

# Appendix C

# Fungi

## C.1 Supplemental methods detail

### C.1.1 Next-generation sequencing

I wet sieved the half of the soil sample destined for NGS rRNA processing on November 23. To reduce cross contamination, sieves were thoroughly rinsed and dried between samples, and a fresh piece of paper was used in place of a sieve pan for each sample. All 40 samples were refrozen simultaneously once processing was complete (total time at room temperature for all samples was 7.5 hours). The samples remained frozen at University of Washington in a -20 °C freezer[1] until January when they were shipped overnight with dry ice to the Fierer Lab at University of Colorado at Boulder.

The Fierer lab extracted DNA from each soil sample using the MoBio PowerSoil DNA[2] isolation kit (MoBio Laboratories, Inc., Carlsbad, CA, USA). Using ITS1-F/ITS2 barcoded primers[3], the

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[1] Freezing soil samples at -80 °C to -20 °C does not affect DNA quality compared with fresh samples (Hart et al., 2015).

[2] Detailed protocol information found in: https://www.cuny.edu/research/sr/undergrad-research/for-faculty/AREM/PowerSoil_DNA_Isolation_Kit_Instruction_Manual.pdf or here: https://www.qiagen.com/us/resources/download.aspx?id=5c00f8e4-c9f5-4544-94fa-653a5b2a6373&lang=en.

[3] A good diagram outlining ITS primers can be found here: https://unite.ut.ee/primers.php

first internal transcribed spacer (ITS1[4]) region of the rRNA operon was amplified in triplicate[5] and sequenced (Crowther et al., 2014). The lab used the PicoGreen dsDNA assay[6] to quantify PCR products from all samples before pooling them in equimolar concentrations. The UltraClean PCR Clean-up Kit[7] was used to clean and concentrate amplicons (MoBio Laboratories, Inc., Carlsbad, CA, USA). An Illumina MiSeq instrument using the paired-end v2 300 cycle MiSeq kit[8] was used to sequence the samples at the University of Colorado Next Generation Sequencing Facility (Illumina, Inc., San Diego, CA, USA). This summary is based on Fierer lab methods described in Barberán et al. (2015), Crowther et al. (2014), and Rojas et al. (2016).

While both forward and reverse reads were obtained from this method, I used only the forward reads for this analysis due to quality issues in the reverse reads causing difficulty pairing the forward and reverse reads. I demultiplexed the forward-read sequences using a Python script[9] written by the Fierer lab (Leff, 2017). I then used the reverse-complimented ITS1-F and ITS2 sequences and the BBDuk Java script from the BBMap package[10] to remove any barcoded primers from the demultiplexed sequences with ktrim = r (Bushnell, 2017).

I trimmed the first 10 base pairs of each read based on FastQC analysis (Babraham Bioinformatics 2016) and filtered the forward reads using dada2[11] (Callahan et al., 2016). Dereplicated reads were assigned to sequence variants based on error rates learned from the dataset, then used to construct a table with sequence counts for each sample. Note that dada2's approach using modeled error rates

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[4] Many, perhaps all, primers have significant drawbacks. Some have fundamental mismatches with certain taxa, and therefore do not detect them reliably; others detect a region that is 'hyper-variable' in some groups, potentially dividing one species into multiple (Hart et al., 2015; Tedersoo et al., 2015). These limitations apply equally across all samples, so while absolute diversity is impacted, between-sample comparisons for my study should not be impacted.

[5] Amplification details from Crowther: "All DNA samples were amplified in triplicate in PCR reactions containing 13 l water, 10 l 5 Prime Hot Master Mix, 0.5 l each of the forward and reverse primers (10 M final concentration), and 1.0 l genomic DNA. Reactions were held at 94 °C for 3 min, with amplification proceeding for 35 cycles at 94 °C for 45 s, 50 °C for 60 s, and 72 °C for 90 s; a final extension of 10 min at 72 °C" (Crowther et al., 2014).

[6] Information on PicoGreen: https://tools.thermofisher.com/content/sfs/manuals/mp07581.pdf .

[7] Detailed protocol information: https://mobio.com/media/wysiwyg/pdfs/protocols/12500.pdf.

[8] Information on the MiSeq Reagent Kit v2: https://support.illumina.com/content/dam/illumina-support/documents/myillumina/cebf8b82-b1d9-4384-a64b-002db4193cbe/miseqreagentkit_v2_reagentprepguide_15034097_b.pdf and the MiSeq system: https://www.illumina.com/content/dam/illumina-marketing/documents/products/datasheets/datasheet_miseq.pdf.

[9] Custom script available at: https://github.com/leffj/helper-code-for-uparse.

[10] Online documentation available online at http://jgi.doe.gov/data-and-tools/bbtools/bb-tools-user-guide/bbmap-guide/ and code available at https://sourceforge.net/projects/bbmap/.

[11] dada2 is an R package that models and corrects Illumina-sequenced amplicon errors and defines sample sequences more accurately than other methods (Callahan et al., 2016). Code and documentation are available online at https://benjjneb.github.io/dada2/index.html.

allows the creation of sequence variants at very high resolution (to single nucleotide differences). Traditional methods use clustering of sequencing reads at ~97% similarity to produce operational taxonomic units (OTUs). Both the increased resolution and the inherent biological meaning of sequence variants make dada2 and sequence variant pipelines a more advantageous choice than OTU pipelines (Callahan et al., 2016).

After removing chimeras[12], the sequence variants were compared with the January 2017 UNITE[13] database using a native implementation of the RDP's naive Bayesian classifier (Callahan et al., 2016; Kõljalg et al., 2013; Wang et al., 2007). Accurate taxonomic matching in UNITE is fundamental to trophic assignment and accurate interpretation of results.

### C.1.2 Sequence variant fungal guild assignment

FUNGuild is an annotation tool that joins species tables with fungal guild information based on distributed expert annotations. In other words, mycologists and published papers provide information about different fungal species (e.g. trophic mode, guild assignments) into a database. Although these are traditionally operational taxonomic unit (OTU) tables, here an SV table was used. The Python based tool is fed a species table with taxonomy attached, parses the taxonomy information, matches the taxonomy with the matching database entry (if present), and outputs the annotated taxa table with fungal guild information attached[14] (Nguyen et al., 2016).

Trophic assignments were based on genus assigned by UNITE for the NGS data or identified in the collections data. We had the greatest level of certainty in this level of taxonomic refinement, as some sequence variants were assigned genus species pairs not known to exist in the United States (e.g. European relatives) and some physical collections could not be identified beyond genus. We excluded sequence variants and collections data that were not identified to genus from trophic analysis as higher taxonomic levels in fungi exhibit significant trophic variation.

I used the online version of the FUNGuild bioinformatic tool available at http://funguild.org to

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[12] Chimeras are hybrid DNA sequences with DNA from more than one organism created during the amplification etc. process (Hart et al., 2015).

[13] UNITE database available online at https://unite.ut.ee/ . Past versions are available for download https://unite.ut.ee/repository.php .

[14] Code to run locally is available on Github: https://github.com/thebateslab/FUNGuild.

annotate my sequence variant table with fungal guild information. All taxa were assumed to be consistent in their trophic guild; that is, a taxon identified as saprotrophic in forests on hardwood would also be saprotrophic in urban areas. As not all genus found in my datasets are represented in FUNGuild, I supplemented FUNGuild with Google Scholar and other scientific databases to fill in the missing trophic information. This list was corrected and added to by Dr. Joseph Ammirati and myself.

### C.1.3 Community data handling and transformations

**NGS dataset:** I did not aggregate the NGS dataset prior to analysis. Analyses were performed with sequence variants as the biological unit of analysis. For guild-specific analyses (saprotroph, pathotroph, symbiotroph), all sequence variants identified to genus or species were included in analysis without aggregation. I used this approach instead of aggregating by genus as UNITE matches may be missing or unreliable, thus making aggregation unreliable (Kõljalg et al., 2013). Aggregation can fail to combine sequence variants without matching UNITE taxonomic information, and generally results either in a dataset with mixed aggregation levels (genus and sequence variants without taxonomic information) or the loss of significant portions of the dataset to achieve uniform aggregation.

The NGS dataset consists of counts of sequence variants for each soil sample. Generally, NGS datasets are overdispersed and have some unique data properties. Due to differential library read sizes between samples (number of rRNA reads per sample), sample variances are not equal (heteroscedasticity). Further, due to the differential amplification of rRNA sequences between species, it is possible to compare a species between sites but not to compare different species within one site[15] (Nguyen et al., 2014).

The common response to these statistical difficulties is to rarefy NGS (usually as OTU instead of SeqVars) data. Rarefying data involves choosing a 'minimum' acceptable library size (total

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[15] Note that the Bray-Curtis dissimilarity index is calculated in such a way that the between species/site limitations are not an issue. The following equation is used to calculate Bray-Curtis dissimilarity: $Bcij = 1 - 2Cij/(Si + Sj)$ Cij is the sum of the lesser values for only those species found at both sites. Si and Sj are the total number of specimens (reads) at both sites. The numerator compares sites within one species, and the denominator is summed library read size, both of which are allowable.

DNA sequence reads for a sample), discarding any sample where the library size is less than this minimum, and for the remaining samples randomly subsampling without replacement such that all samples are equal in size to the minimum library size (Barberán et al., 2015; McMurdie and Holmes, 2014; e.g. see Rojas et al., 2016). Rarefaction is statistically inefficient (loss of statistical power, increasing Type-II error) and statistically inadmissible (it requires the researcher to omit available valid data according to an arbitrary library size minimum, and adds a random step adding artificial uncertainty). Rarefaction also does not adequately address the overdispersion found in NGS data (increasing Type-I error), can result in a high rate of false positives, and 'solves' heteroscedasticity by equalizing variances based on the largest (worst) value (McMurdie and Holmes, 2014). Overall, rarefaction is likely to result in a dataset that does not represent the original communities (Hart et al., 2015).

I removed highly rare sequence variants (global $n \leqslant 10$) from my dataset. Rare sequences have low global read depth—that is, they are detected once or only a few times across the entire dataset. For NGS derived datasets, rare sequences may include PCR/sequencing artifacts or true species detections. However, unless a study is determining precise biodiversity estimates, discarding rare sequences is unlikely to alter the results of downstream community analysis (Brown et al., 2015).

In contrast with most other work on the microbiome, I did not rarefy my NGS dataset to an even library size prior to analysis. Instead, prior to PERMANOVA, NMDS, and TITAN analysis I applied the square root transformation to the data to downweight the importance of the most abundant SeqVars (Nguyen et al., 2014). For univariate analysis, I calculated effective number of species (effective species richness; defined as exp(Shannon entropy); see Jost, 2006) for each sample as the response variable.

**Collections dataset:** Collections were aggregated to genus, as this was judged the most accurate resolution for identification. Unlike the NGS dataset where sequence variants have biological meaning and are separated based on true genetic differences, the identification to species of physical samples relies on high quality collected samples. Additionally, since it is not possible to determine the number of distinct organisms of each fungal species present at each site, collections data is presence/absence data. I did not use any rare species filtering for my collections based dataset, and no further transformations were applied prior to multivariate analysis. As with the NGS data, I calculated effective number of species (defined as exp(Shannon entropy); see Jost, 2006) for the response variable in univariate analysis.

## C.2 Summary of soil chemistry

Summary of soil chemistry values as sampled from grass, mulch, and unmanaged ground cover within 17 sites.

Summary of area-weighted soil chemistry values for 17 sampled sites. These values were used in both NGS and mushroom collection dataset analysis.

Table C.1: Summary statistics for soil chemistry as sampled. Note that pH median, mean, and standard deviation are reported on the pH values themselves, and not calculated based on the H+. The values are similar (<.2 difference) and sufficient for descriptive statistics.

| | Minimum | Maximum | Median | Mean | Std Dev |
|---|---|---|---|---|---|
| pH | | | | | |
| Grass | 4.44 | 6.08 | 5.41 | 5.39 | 0.56 |
| Mulch | 4.51 | 6.42 | 5.71 | 5.64 | 0.53 |
| Unmanaged | 5.07 | 6.04 | 5.72 | 5.64 | 0.45 |
| Pct Carbon | | | | | |
| Grass | 2.52 | 11.34 | 6.6 | 6.24 | 2.71 |
| Mulch | 2.22 | 15.9 | 5.52 | 6.63 | 3.59 |
| Unmanaged | 3.57 | 11.75 | 5.02 | 6.34 | 3.74 |
| Pct Nitrogen | | | | | |
| Grass | 0.12 | 0.61 | 0.38 | 0.37 | 0.16 |
| Mulch | 0.09 | 0.63 | 0.18 | 0.23 | 0.13 |
| Unmanaged | 0.14 | 0.47 | 0.2 | 0.25 | 0.15 |
| Carbon:Nitrogen | | | | | |
| Grass | 13.41 | 21.36 | 17.42 | 17.29 | 2.33 |
| Mulch | 18.96 | 47.6 | 31.37 | 31.03 | 9.06 |
| Unmanaged | 21.27 | 28.98 | 25.33 | 25.23 | 3.16 |

Table C.2: Summary statistics for soil nutrients used in analysis of mushroom collection dataset. Values are area-weighted.

| Variable | Minimum | Maximum | Median | Mean | Std Dev |
|---|---|---|---|---|---|
| Area Weighted pH | 4.51 | 6.41 | 5.44 | 5.47 | 0.58 |
| Area Weighted % Carbon | 2.33 | 15.9 | 6.12 | 6.76 | 3.22 |
| Area Weighted % Nitrogen | 0.1 | 0.5 | 0.35 | 0.29 | 0.14 |
| Carbon:Nitrogen | 15.18 | 43.92 | 23.65 | 25.59 | 8.47 |

## C.3 Univariate comparison tables

Univariate AICc results for the mushroom collections dataset.

Table C.3: Best supported models for univariate collections dataset. Note comparison with Median HH Income.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---:|---:|---:|---:|
| Visits, Percent Impervious (on site), and Appraised Land Value per Acre | 0.776 | 17.34 | 0.00 | 0.0065 |
| Visits, Dead Wood, and Appraised Land Value per Acr | 0.776 | 17.35 | 0.00 | 0.0000 |
| Visits, Pct Impervious, Dead Wood, Appraised Land Value per Acre | 0.799 | 13.95 | 0.00 | 1.6805 |
| Visits and Median HH Income ($) | 0.306 | 3.52 | 0.05 | 18.2607 |

## C.4 Multivariate comparison tables

AICc values should be interpreted with caution, as models of the form y ~ non-significant variables had Δ AICc of < 1. A more rigorous cutoff for interpreting equal support may be necessary, or AICc formulas for multivariate ANOVA may require a different derivation from univariate forms.

Table C.4: Best supported models for multivariate collections dataset, all fungi collected. Note comparison with Median HH Income. Soil variables cannot be compared with other variables due to different N.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Tree Cluster | 0.100496 | 1.899304 | 0.004 | 0.22907 |
| Acres | 0.084231 | 1.563642 | 0.045 | 0.569553 |
| Percent Impervious (on site) | 0.110961 | 2.121781 | 0.004 | 0.006714 |
| Native Conifer Density | 0.111276 | 2.128539 | 0.004 | 0 |
| Mulch | 0.096179 | 1.809028 | 0.024 | 0.320045 |
| Native Shrub ESR | 0.083279 | 1.544346 | 0.046 | 0.589313 |
| Stand Predates Development | 0.092898 | 1.741008 | 0.008 | 0.388879 |
| Tree Cluster and Percent Impervious | 0.190158 | 1.878464 | 0.001 | 1.083999 |
| Area (ac) and Percent Impervious | 0.193233 | 1.916116 | 0.002 | 1.011717 |
| Area and Native Conifer Density | 0.188064 | 1.852989 | 0.001 | 1.133061 |
| Area and Mulching | 0.18184 | 1.778042 | 0.005 | 1.278136 |
| Percent Impervious and Native Conifer Density | 0.177348 | 1.724649 | 0.003 | 1.382171 |
| Percent Impervious and Stand Predates Development | 0.178995 | 1.744153 | 0.004 | 1.344103 |
| Median HH Income ($) | 0.068322 | 1.246651 | 0.2 | 0.896797 |
| — | — | — | — | — |
| Weighted C:N | 0.098115 | 1.631829 | 0.032 | 0.048802 |
| Weighted N% | 0.1007 | 1.679644 | 0.026 | 0 |
| Weighted C:N and Weighted N% | 0.186237 | 1.602017 | 0.011 | 1.289899 |

Table C.5: Best supported models for multivariate collections dataset, saprobic fungi collected. Note comparison with Median HH Income. Soil variables cannot be compared with other variables due to different N.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Acres | 0.084231 | 1.563642 | 0.038 | 0.569553 |
| Percent Impervious (on site) | 0.110961 | 2.121781 | 0.002 | 0.006714 |
| Mulch | 0.096179 | 1.809028 | 0.027 | 0.320045 |
| Stand Predates Development | 0.092898 | 1.741008 | 0.015 | 0.388879 |
| Native Conifer Density | 0.111276 | 2.128539 | 0.001 | 0 |
| Tree Cluster | 0.100496 | 1.899304 | 0.001 | 0.22907 |
| Area (ac) and Percent Impervious | 0.193233 | 1.916116 | 0.002 | 1.011717 |
| Area and Mulch | 0.18184 | 1.778042 | 0.004 | 1.278136 |
| Area and Native Conifer Density | 0.188064 | 1.852989 | 0.002 | 1.133061 |
| Percent Impervious and Stand Predates Development | 0.178995 | 1.744153 | 0.002 | 1.344103 |
| Percent Impervious and Native Confier Density | 0.177348 | 1.724649 | 0.002 | 1.382171 |
| Percent Impervious and Tree Cluster | 0.190158 | 1.878464 | 0.001 | 1.083999 |
| Median HH Income ($) | 0.068322 | 1.246651 | 0.227 | 0.896797 |
| — | — | — | — | — |
| Weighted C:N | 0.118614 | 2.018659 | 0.012 | 0 |
| Weighted N % | 0.104828 | 1.756555 | 0.022 | 0.263854 |

Table C.6: Best supported models for multivariate collections dataset, symbiotic fungi collected. Note comparison with Median HH Income. Soil variables cannot be compared with other variables due to different N.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Irrigation | 0.175484 | 1.702656 | 0.015 | 0.528391 |
| Median HH Income ($) | 0.068322 | 1.246651 | 0.205 | 0 |
| — | — | — | — | — |
| Weighted N % | 0.116386 | 1.975734 | 0.046 | 0 |

Table C.7: Best supported models for multivariate collections dataset, pathotrophic fungi collected. Note comparison with Median HH Income. Comparison with other trophic sub-groups not possible due to different N. Soil variables cannot be compared with other variables due to different N.

| Model | Var Explnd | Pseudo-F | p-value | Delta AICc |
|---|---|---|---|---|
| Median 7 day Avg Temp (F) and Percent Impervious | 0.449068 | 4.890635 | 0.001 | 0.380517 |
| Median 7 day Avg Temp, Pct Impervious, and Median DF Height (m) | 0.583578 | 5.138511 | 0.001 | 0 |
| Median 7 day Avg Temp, Pct Impervious, and Tree Cluster | 0.576816 | 4.997804 | 0.001 | 0.241638 |
| Median 7 day Avg Temp and Median HH Income ($) | 0.224971 | 1.741645 | 0.106 | 5.499852 |
| — | — | — | — | — |
| Weighted C % | 0.204845 | 2.833774 | 0.034 | 0 |
| Weighted N % | 0.196218 | 2.685298 | 0.04 | 0.140282 |

Table C.8: Best supported models for multivariate NGS dataset, all fungi sequence variants.

| Model | Pseudo-_F_ | p-value | Adjusted p-value | Delta AICc |
|---|---|---|---|---|
| Weighted pH | 1.46 | 0.003 | 0.018 | 0.0000 |
| Stands Predate Development | 1.28 | 0.006 | 0.030 | 0.1821 |
| Weighted Carbon (%) | 1.37 | 0.124 | 0.248 | 0.0892 |
| Native Shrub ESR | 1.30 | 0.020 | 0.080 | 0.1618 |

Table C.9: Best supported models for multivariate NGS dataset, saprotrophic fungi sequence variants.

| Model | Var Explnd | Pseudo-_F_ | p-value | Delta AICc |
|---|---|---|---|---|
| Weighted pH | 0.0882 | 1.45 | 0.003 | 0.000 |
| Weighted C:N | 0.0827 | 1.35 | 0.038 | 0.102 |
| Tree Cluster | 0.0775 | 1.26 | 0.025 | 0.198 |
| Native Shrub ESR | 0.0815 | 1.33 | 0.027 | 0.124 |

Table C.10: Best supported models for multivariate NGS dataset, symbiotrophic fungi sequence variants.

| Model | Var Explnd | Pseudo-_F_ | p-value | Delta AICc |
|---|---|---|---|---|
| Weighted C:N | 0.0800 | 1.30 | 0.038 | 0.0852 |
| Weighted pH | 0.0835 | 1.37 | 0.016 | 0.0216 |
| Shrub Native ESR | 0.0799 | 1.30 | 0.036 | 0.0880 |
| Stand Predates Development | 0.0846 | 1.39 | 0.005 | 0.0000 |

Table C.11: Best supported models for multivariate NGS dataset, pathotrophic fungi sequence variants.

| Model | Var Explnd | Pseudo-_F_ | p-value | Delta AICc |
|---|---|---|---|---|
| Tree Cluster | 0.0719 | 1.16 | 0.036 | 0.356 |
| Native Shrub ESR | 0.0819 | 1.34 | 0.031 | 0.172 |
| Weighted C:N | 0.0834 | 1.37 | 0.023 | 0.144 |
| Weighted pH | 0.0912 | 1.50 | 0.002 | 0.000 |

## C.5 TITAN results

### C.5.1 Fungal ecological preference: significant continuous development and landscape variables

For all graphs, pure and reliable (robust) negatively responding taxa are shown on the left axis, and robust positively responding taxa are shown on the right axis (z-/z+ respectively). Change point symbols (filled or empty circles for z-/z+) are plotted at the median of the bootstrap replicates using the median z-score instead of the observed value. The horizontal lines extending from each change point (solid or dashed lines for z-/z+) represent the 5%-95% quantiles based on the bootstrapped change point distribution. The vertical lines represent the 50% quantile or median sum(z) of the change points for the increasing or decreasing community, determined by resampling the observed data. The hashed box represents the 5%-95% quantiles of sum(z) of change points for the increasing and decreasing community. Unless otherwise indicated, these change points corresponding to declining/increasing taxa for the robust taxa. For all graphs, a red vertical line plus pink hash is used for the “more urban” end of the environmental gradient, while a green vertical line plus gray hash is used for the “less urban” end of the environmental gradient. Please see [https://cran.r-project.org/web/packages/TITAN2/vignettes/glades.TITAN.html] for more information.

Underneath each change point graph is a count-based histogram of the surveyed sites over the environmental gradient. These are provided to show where along the environmental gradient there are gaps in surveyed sites. Gaps in sampling the environmental gradient may increase the width of the bootstrapped change point distribution for each taxon (horizontal lines).

**Percent impervious surface on site:** Fewer taxa had positive associations with increasing percent impervious on site in both NGS and collections datasets. A synchronous change in both increasing (z+) and decreasing (z-) taxa was observed at approximately 70% impervious surface on site for the NGS dataset. NGS and collections datasets provided very similar results; median filtered sum(z-) was 0.71 for the NGS dataset and 0.679 for the collections data; median filtered sum(z+) was 0.757 for the NGS dataset and unfiltered sum(z+) was 0.723 for the collections data.

The bootstrap frequency distributions of decreasing (z-) taxa with change points around 70% generally extended towards lower, but not higher, amounts of impervious surface. Overall, there is evidence for a community threshold at approximately 70% impervious surface. Additionally, below 70% impervious surface on site there is a wide, asynchronous distribution of decreasing (z-) taxa change points, suggesting that additional taxa drop out gradually. Relatively few sites were sampled between 60-70% and below 50% impervious surface. Further sampling of office developments with lower % impervious surface on site may reveal additional community thresholds at these levels.

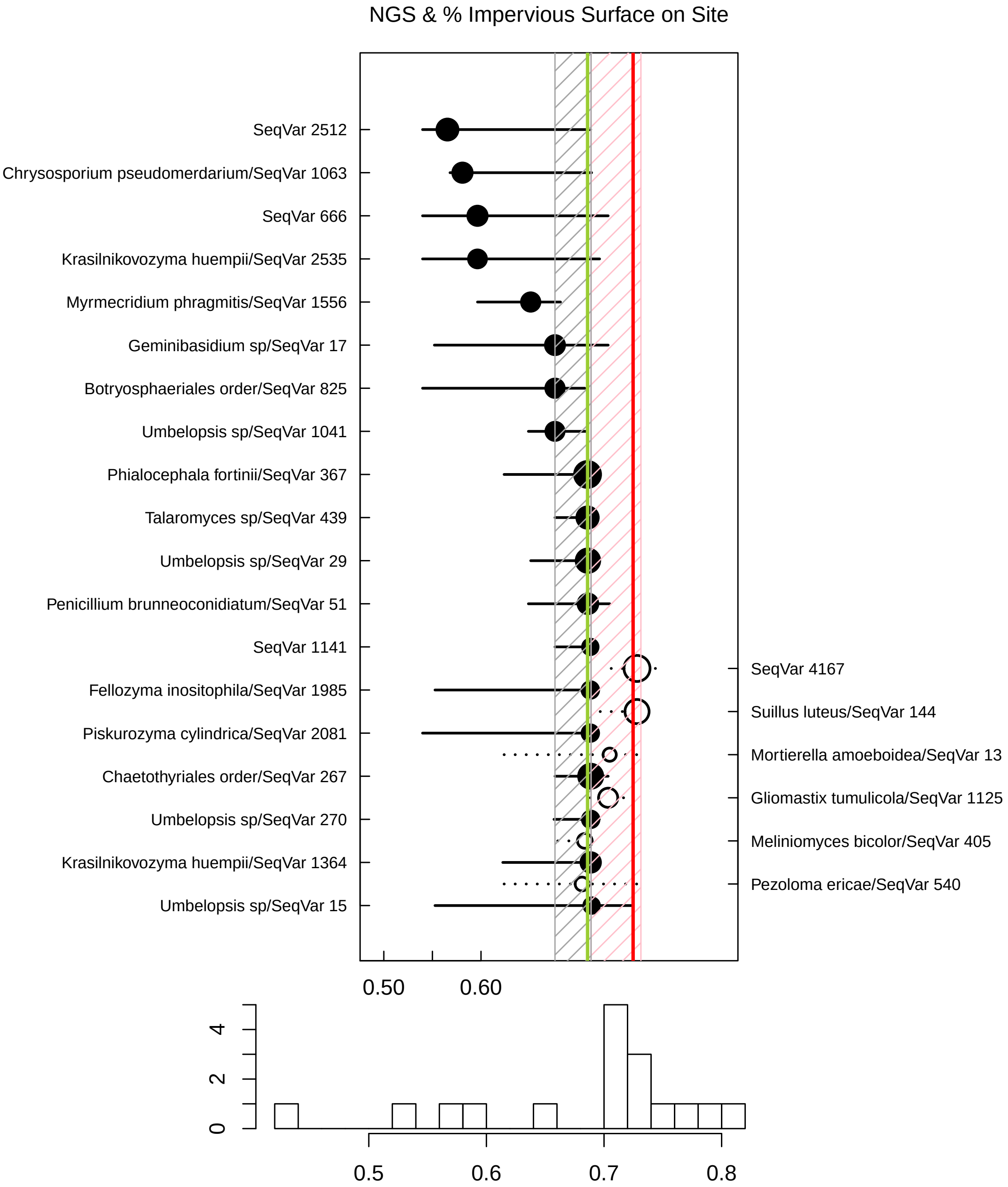

Figure C.1: NGS data TITAN results for impervious surface on site.

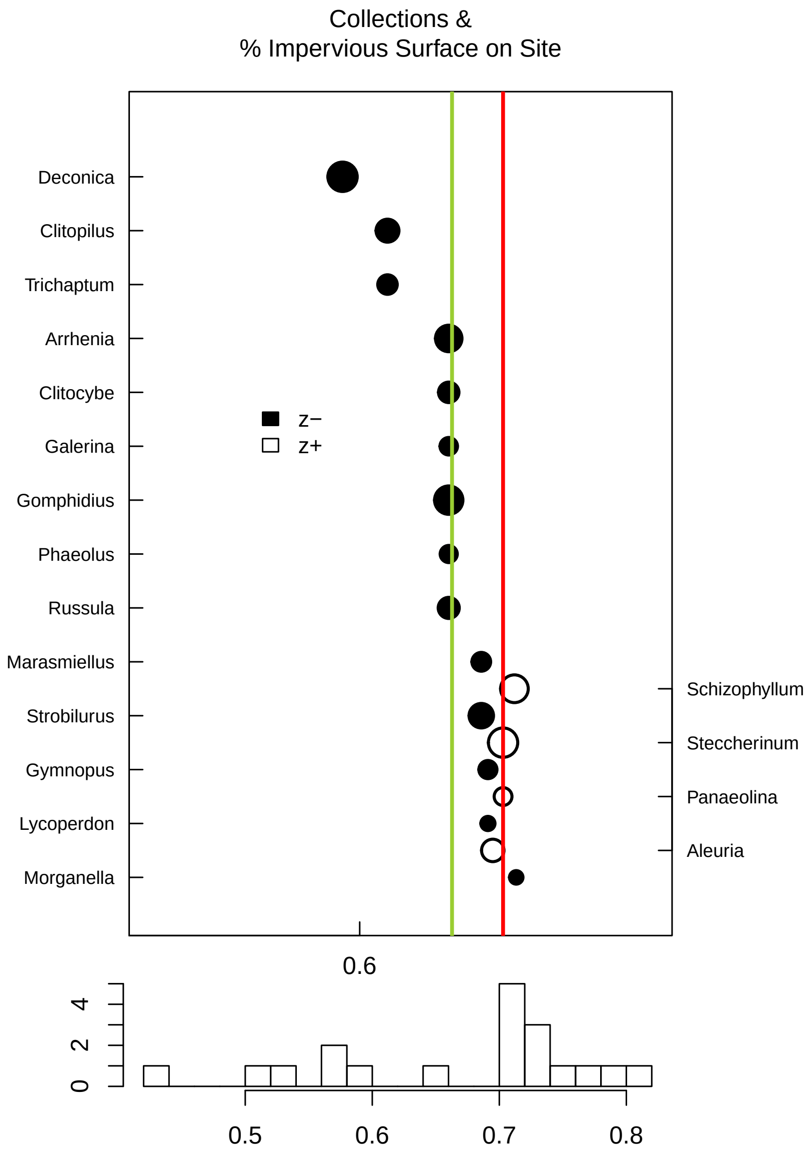

Figure C.2: Mushroom collections data TITAN results for impervious surface on site.

**Median Dominant Douglas-fir Height (m):** More taxa were associated with increasing median dominant Douglas-fir height (m) in both NGS and collections datasets. In the NGS dataset, negative (z-) indicator taxa declined gradually between 5 and 25 m. Median filtered sum(z-) was 19.4. Change points for these z- taxa also have relatively wide bootstrap intervals. The asynchrony of change points for z- taxa is not consistent with an ecological community threshold among fungi associated with smaller Douglas-fir.

In contrast, positive (z+) indicator taxa increased fairly sharply between 27 and 37 m. The median filtered sum(z+) was 35.6. The sharp accumulation of taxa with increasing median height and relatively narrow change point bootstrap intervals suggests that there may be a defined ecological community threshold with increasing median Douglas-fir height around 35 m.

Analysis using the collections dataset should be interpreted with caution due to the low number of observations and of pure and reliable taxa (Figure C.4). A similar pattern as in the NGS dataset is apparent when including all taxa with significant p-values $< 0.05$ instead of only pure and reliable taxa. Median filtered sum(z-) was 22.7 and median filtered sum(z+) was 30.1 for the collections data.

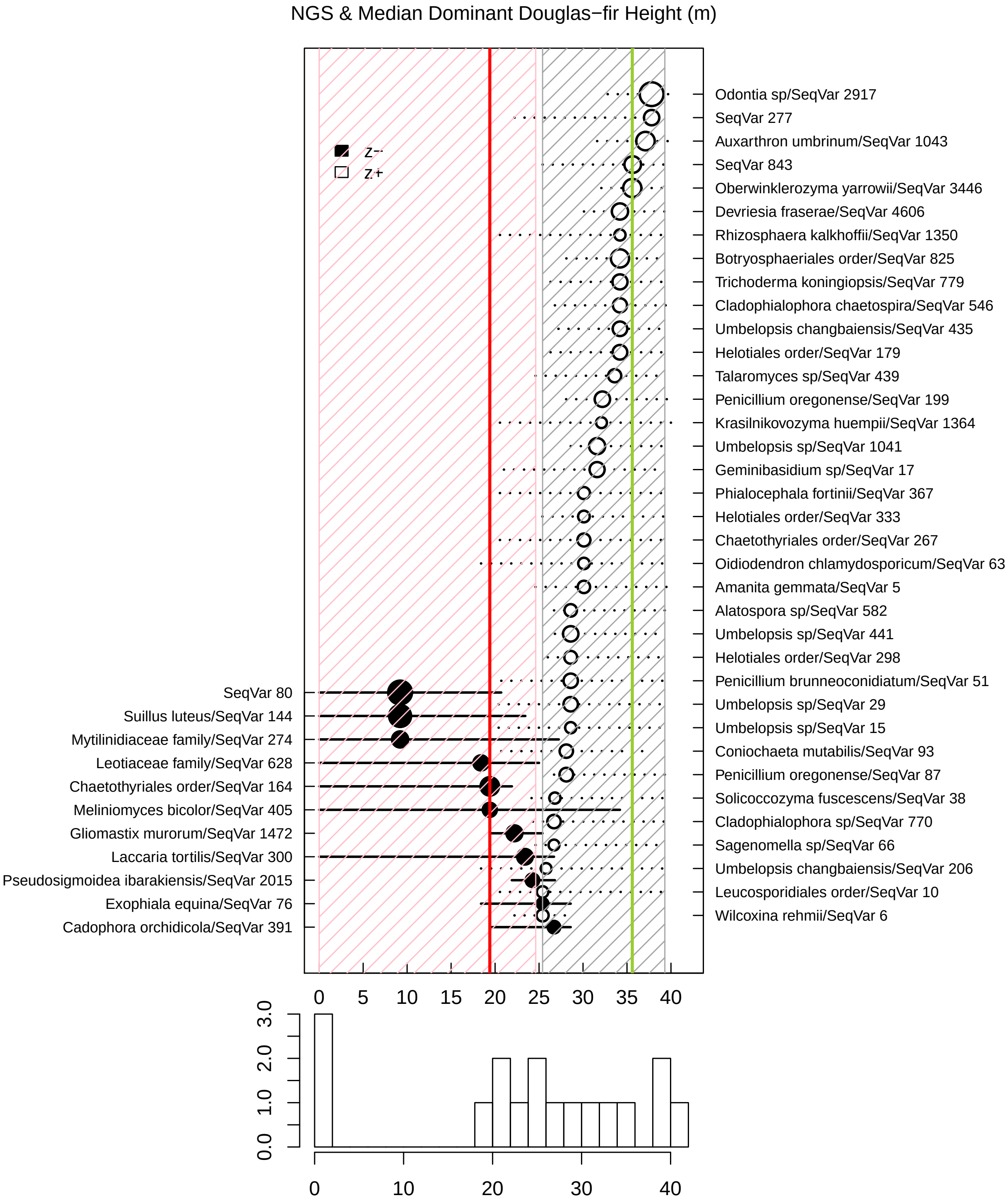

Figure C.3: NGS data TITAN results for median dominant Douglas-fir height.

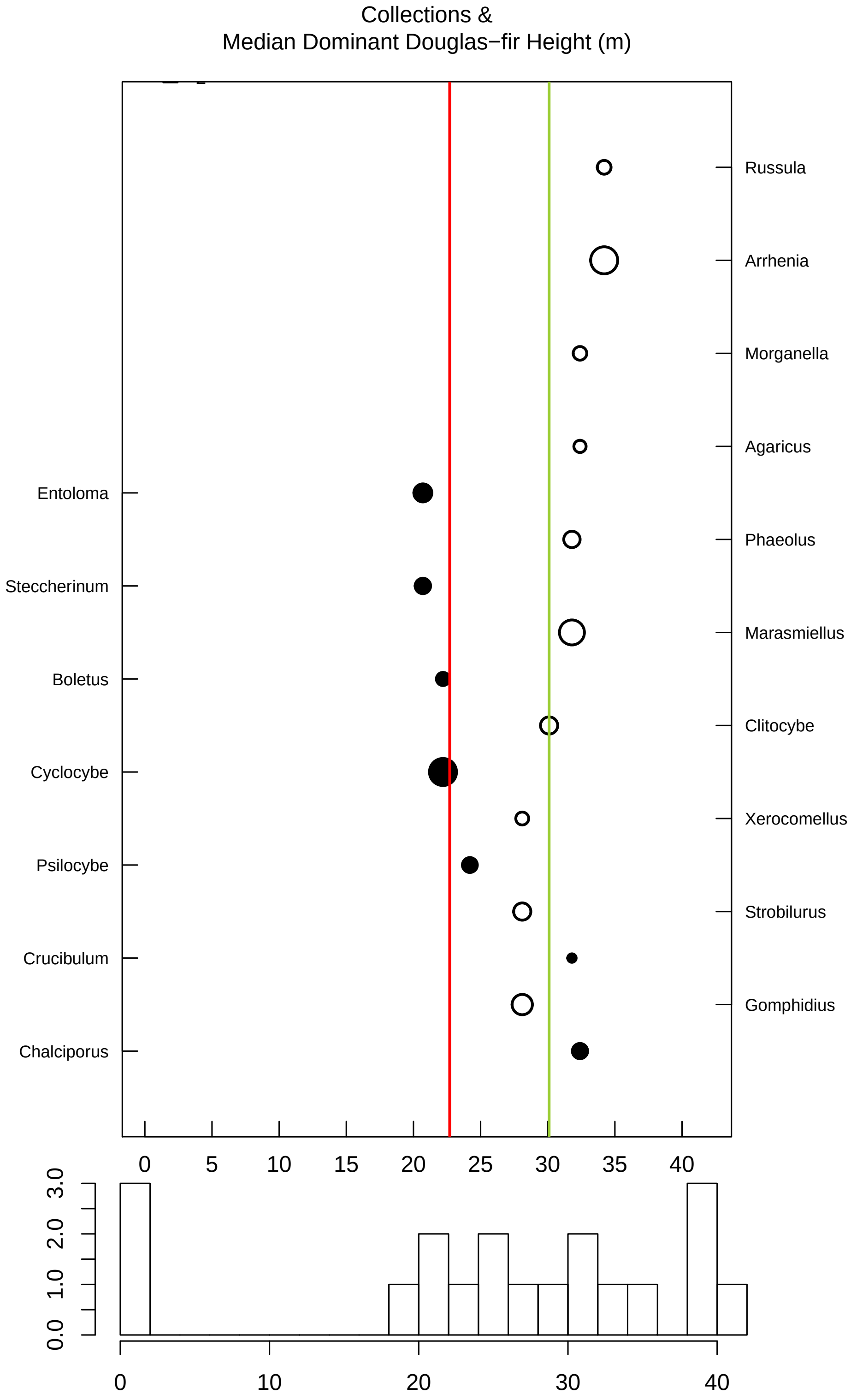

Figure C.4: Mushroom collections data TITAN results for median dominant Douglas-fir height.

**Native Conifer Density (trees/acre):** In both NGS and collections datasets, there were more positive (z+) indicator taxa then negative (z-). In both datasets, negative indicator taxa declined sharply between 0-4 native conifer trees/acre, resulting in a median filtered sum(z-) of NGS = 4.677 trees/acre and collections = 22.271. The overlap of individual taxon change points provides evidence for an ecological community threshold.

Positive (z+) indicator taxa exhibit two sharp inclines, the first between 22-25 trees/acre and the second between 40-50 trees/acre. NGS data showed evidence of the first (median filtered sum(z+) is 23.595), and collections dataset of both (median filtered sum(z+) was 23.595). Plots of the sum(z) also support two discrete taxa change points. For the NGS dataset, Distribution of z+ bootstrap replicates is wide, though relatively few observations at higher native conifer densities suggest interpreting these bootstrap intervals with caution.

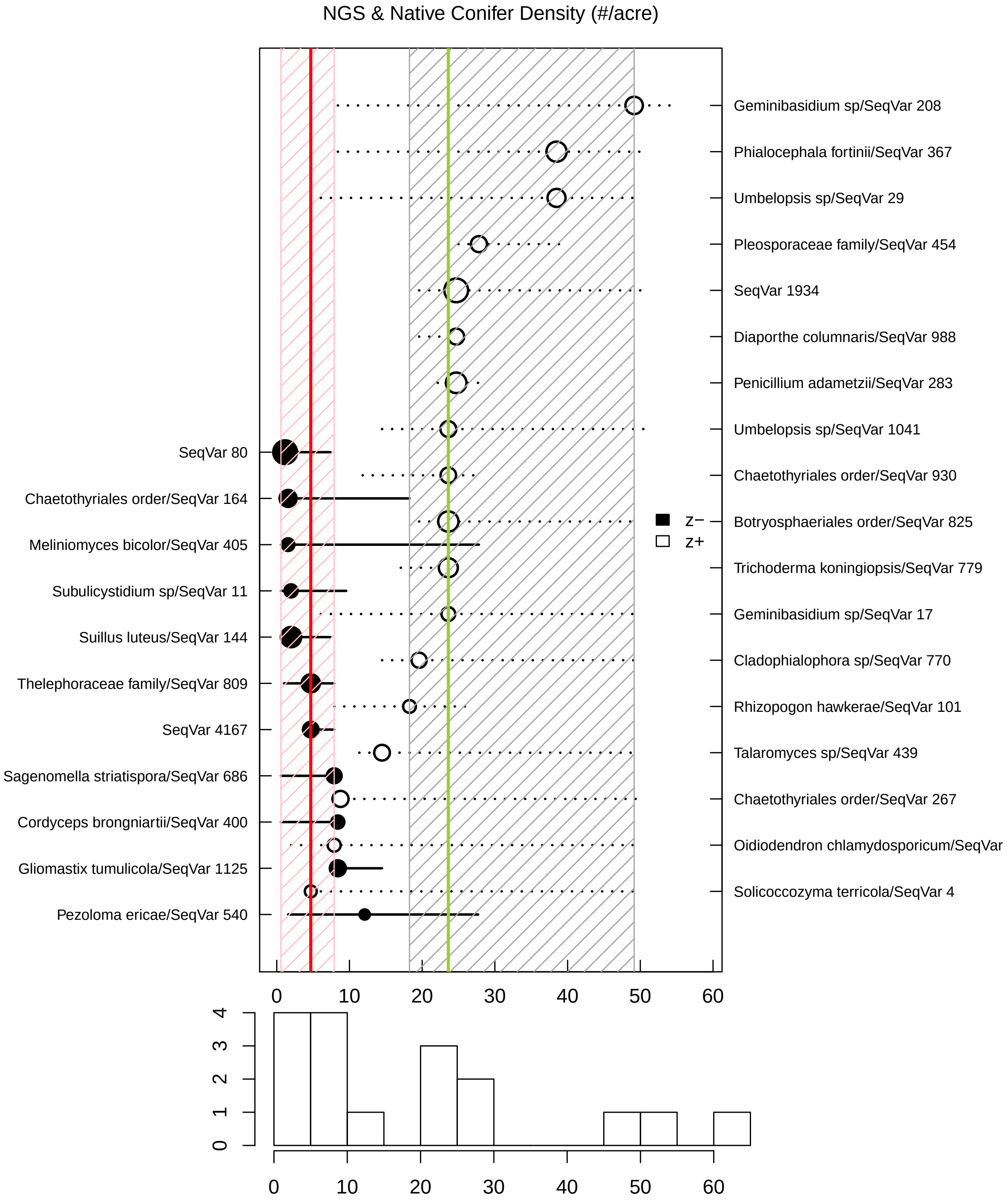

Figure C.5: NGS data TITAN results for native conifer density.

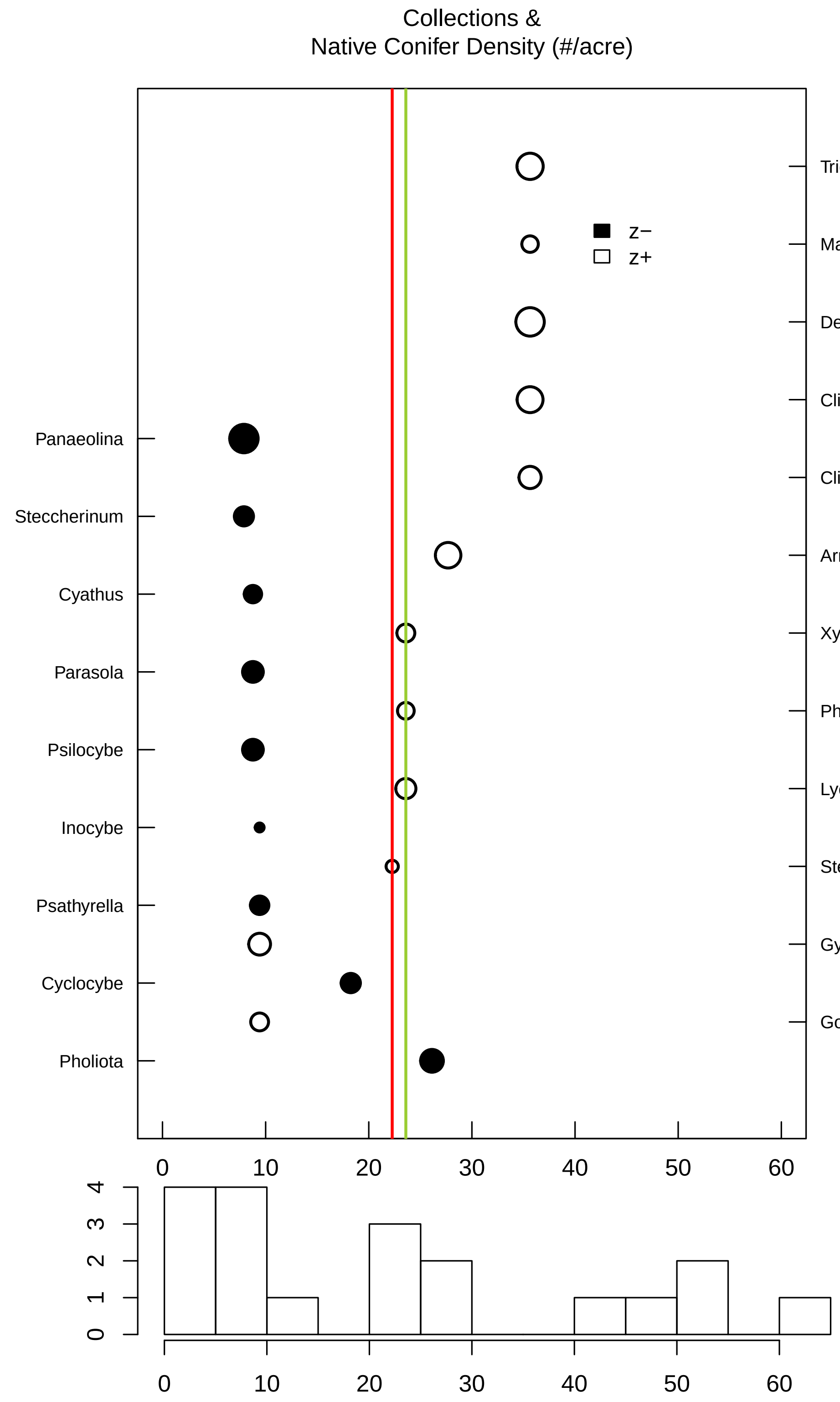

Figure C.6: Mushroom collections data TITAN results for native conifer density.

**Shrub Effective Species Richness:** There were more positive (z+) indicator taxa than negative (z-) for both NGS and collections datasets. For the NGS dataset, positive (z+) indicator taxa increased sharply between 3.5-4.0 effective species, with a median filtered sum(z+) of 3.06 effective species. The synchrony of change provides support for an ecological community threshold. Additionally, the widths of the distribution of bootstrap replicates were generally narrow, suggesting this threshold involves relatively sensitive taxa. Conversely, negative (z-) indicator taxa dropped out in an approximately linear sequence between 1.5-3.0 effective species, suggesting an asynchronous distribution of negative (z-) taxa change points. The median filtered sum(z-) is 1.922 effective species. Bootstrap replicates for negative taxa are generally wide, though fewer samples between 1-3 effective species suggest interpreting the results with caution.

For the collections dataset, positive (z+) indicator taxa showed a similar pattern, with evidence of an ecological community threshold between 3.7-4.2 effective species (Figure). The median filtered sum(z+) for this dataset was 2.731 effective species. Negative (z-) indicator taxa were not well defined and an unfiltered median sum(z-) could not be calculated due to too few pure and reliable taxa and observations.

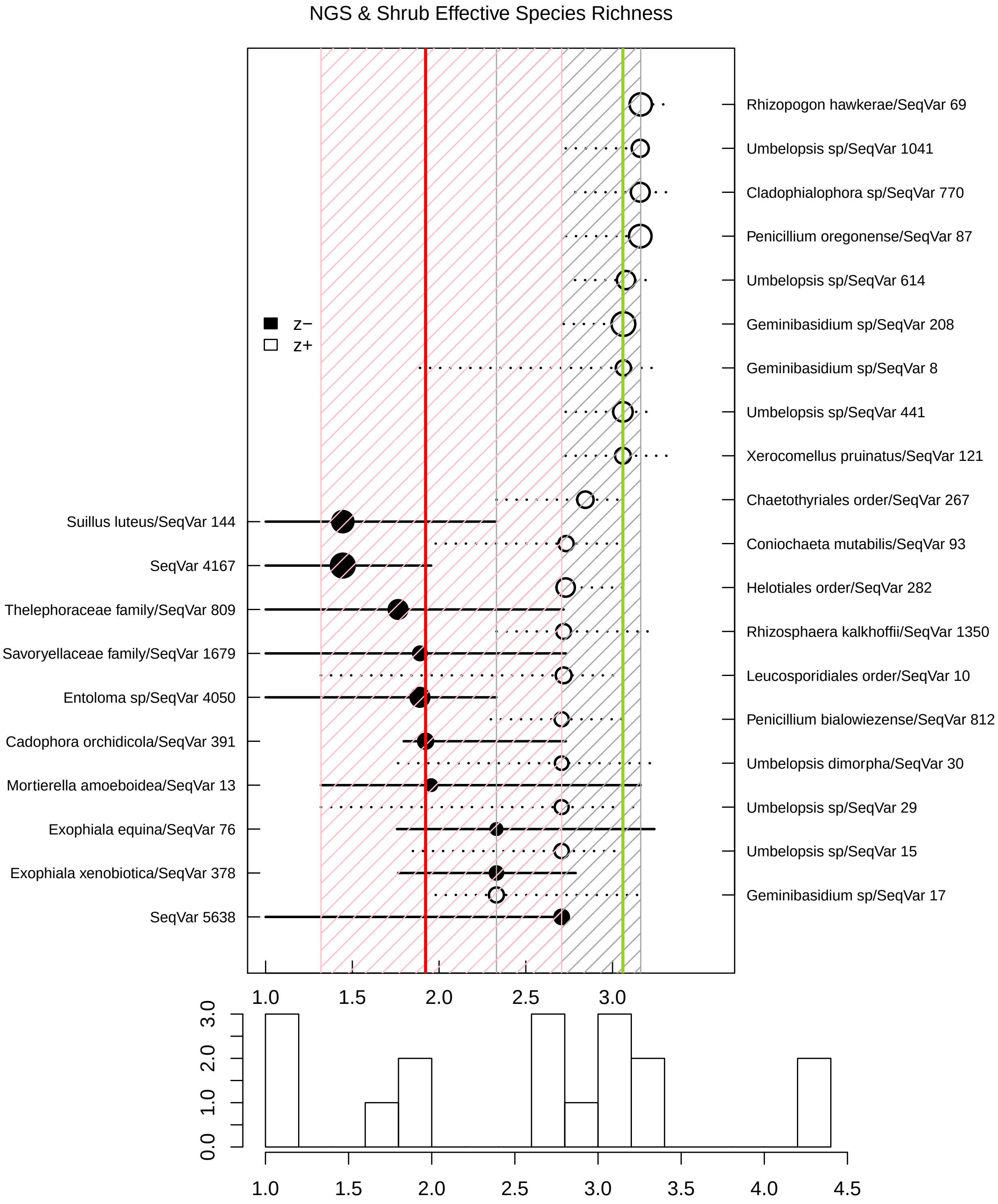

Figure C.7: NGS data TITAN results for native shrub effective species richness.

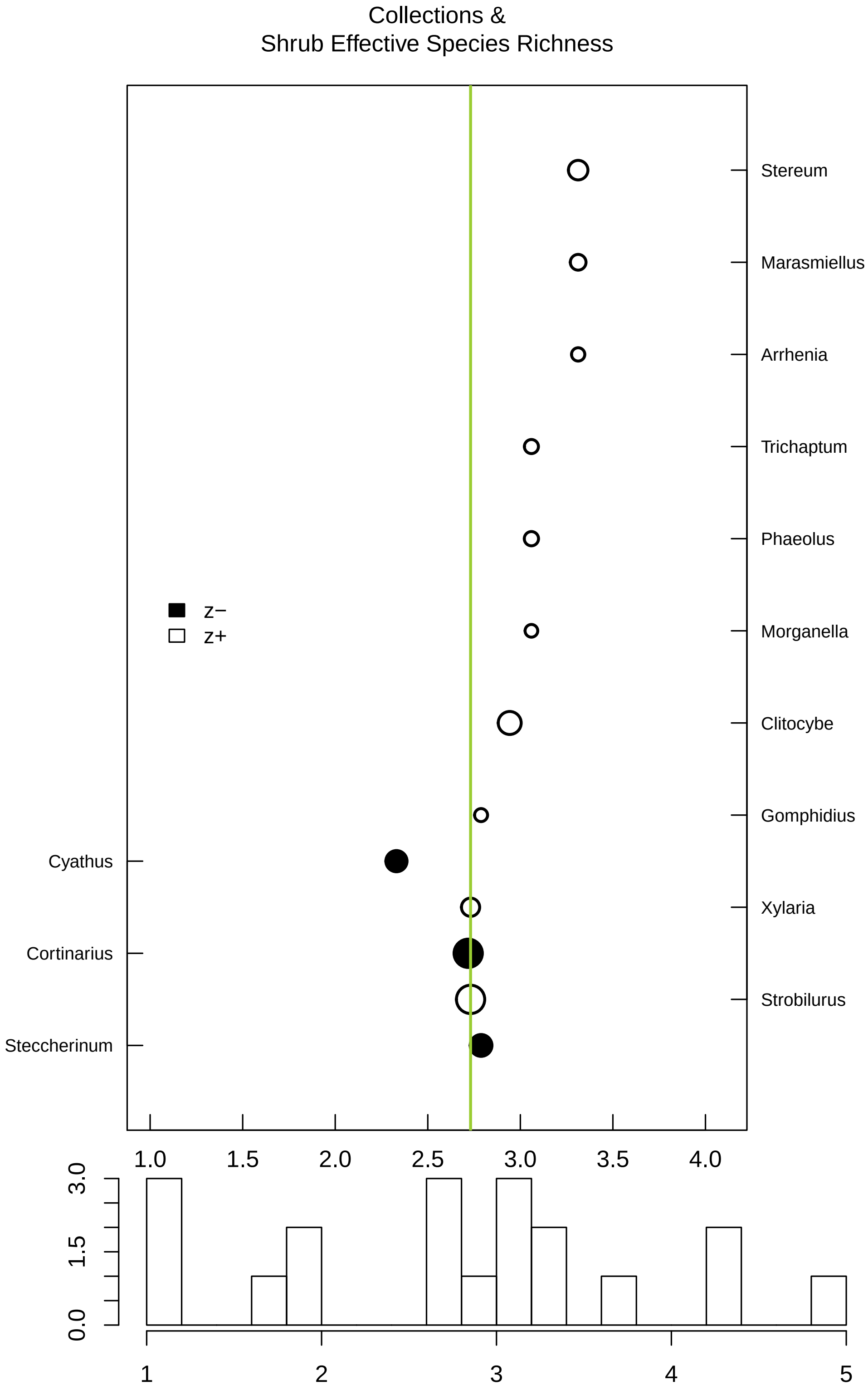

Figure C.8: Mushroom collections data TITAN results for native shrub effective species richness.

**Native Shrub Density:** The NGS, but not the collections dataset, found more positive (z+) indicator taxa than negative (z-) taxa. Most of the detected negative (z-) indicator taxa in the NGS dataset declined in a sharp linear pattern between 0-20 native shrubs/acre, with a median filtered sum(z-) of 10.662 shrubs/acre. This relatively confined band of nearly all detected negative (z-) taxa suggest an ecological community threshold.

Detected positive (z+) indicator taxa exhibit two disjoint clusters of change points in response to increasing native shrub density: the first at 20 native shrubs/acre and the second around 80 shrubs per acre. Median filtered sum(z+) falls in the middle at 57.08, with wide bounds (grey box, Figure). The first cluster of change points matches with the ecological community threshold suggested by negative (z-) indicator taxa. The second suggest an additional community change at higher shrub densities. However, that few sites surveyed had greater than 50 native shrubs/acre limits interpretability both of this second ecological community threshold and the width of the distribution of bootstrap replicates.

Both few detected pure and reliable taxa and the low number of observations limit interpretability of the collections dataset. For the negative (z-) taxa, the collections dataset suggests a similar pattern as the NGS dataset with some evidence of an ecological community threshold at about 20 native shrubs/acre. However, median sum(z-) for the filtered data could not be calculated, for unfiltered the median sum(z-) is 17.491. Positive taxa appear to increase either in discrete clusters as with the NGS data or linearly with increasing shrub density. Median filtered sum(z+) is 41.345.

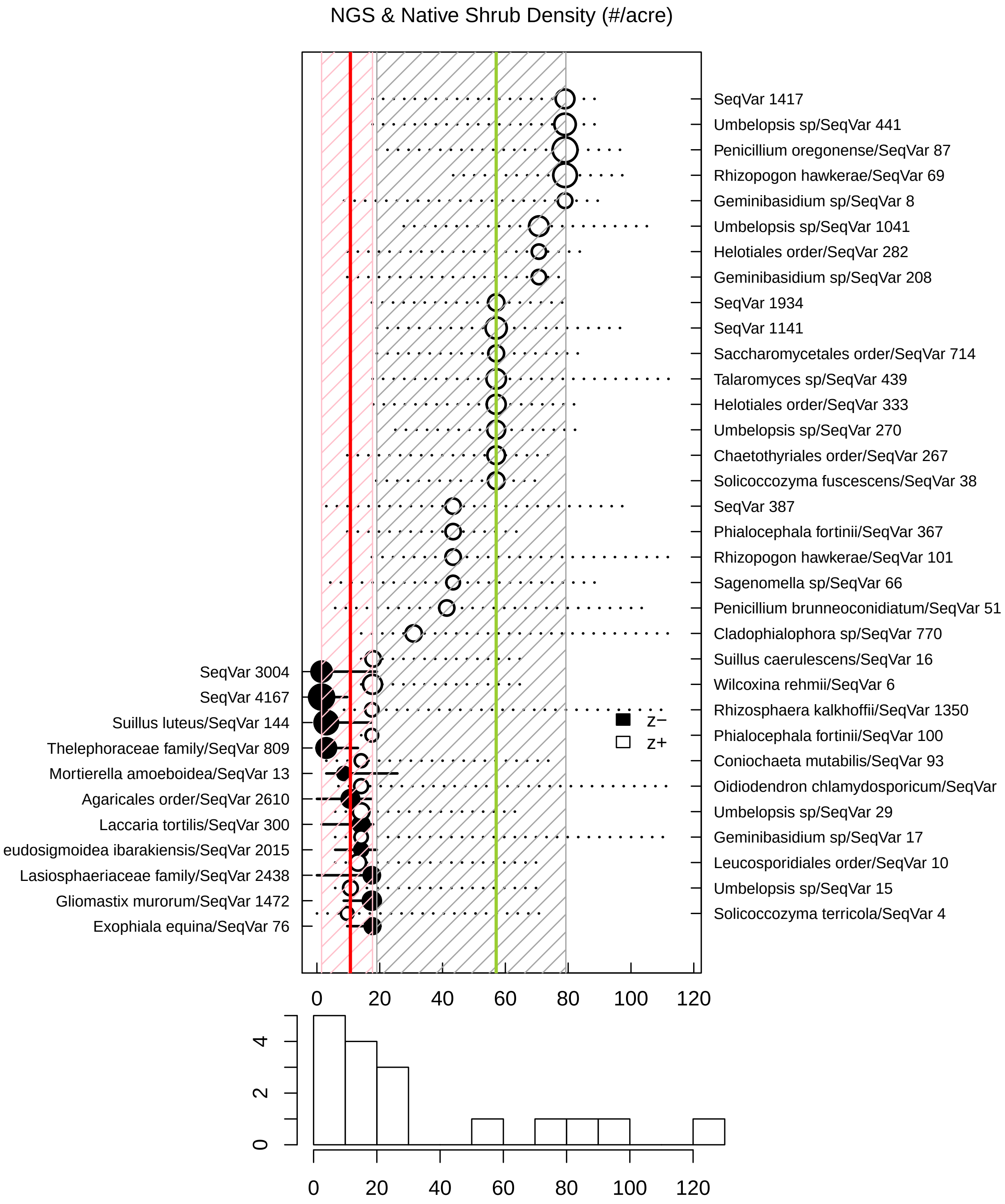

Figure C.9: NGS data TITAN results for native shrub density.

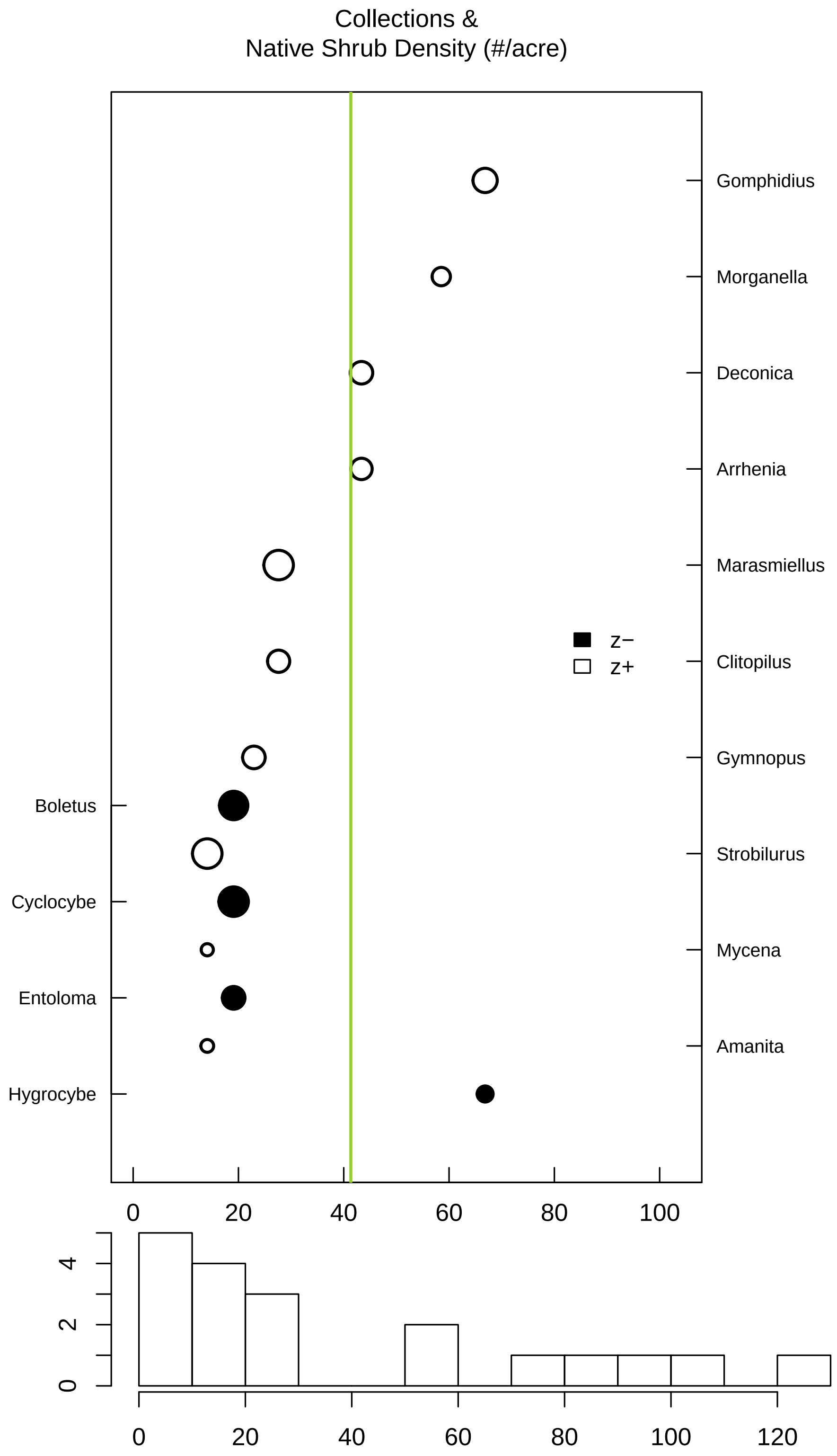

Figure C.10: Mushroom collections data TITAN results for native shrub density.

### C.5.2 Fungal ecological preference: Soil chemistry gradients

**pH:** Approximately equal numbers of negative (z-) and positive (z+) indicator taxa were identified along the pH gradient. Both categories of indicator taxa experienced sharp changes around pH 5.5. Median filtered sum(z-) was 5.53; median filtered sum(z+) was 5.855 for the NGS dataset. Additional taxa fell out (z-) or were added (z+) in an approximately linear sequence both below and above pH 5.5. This synchronous change in taxa is consistent with an ecological community threshold.

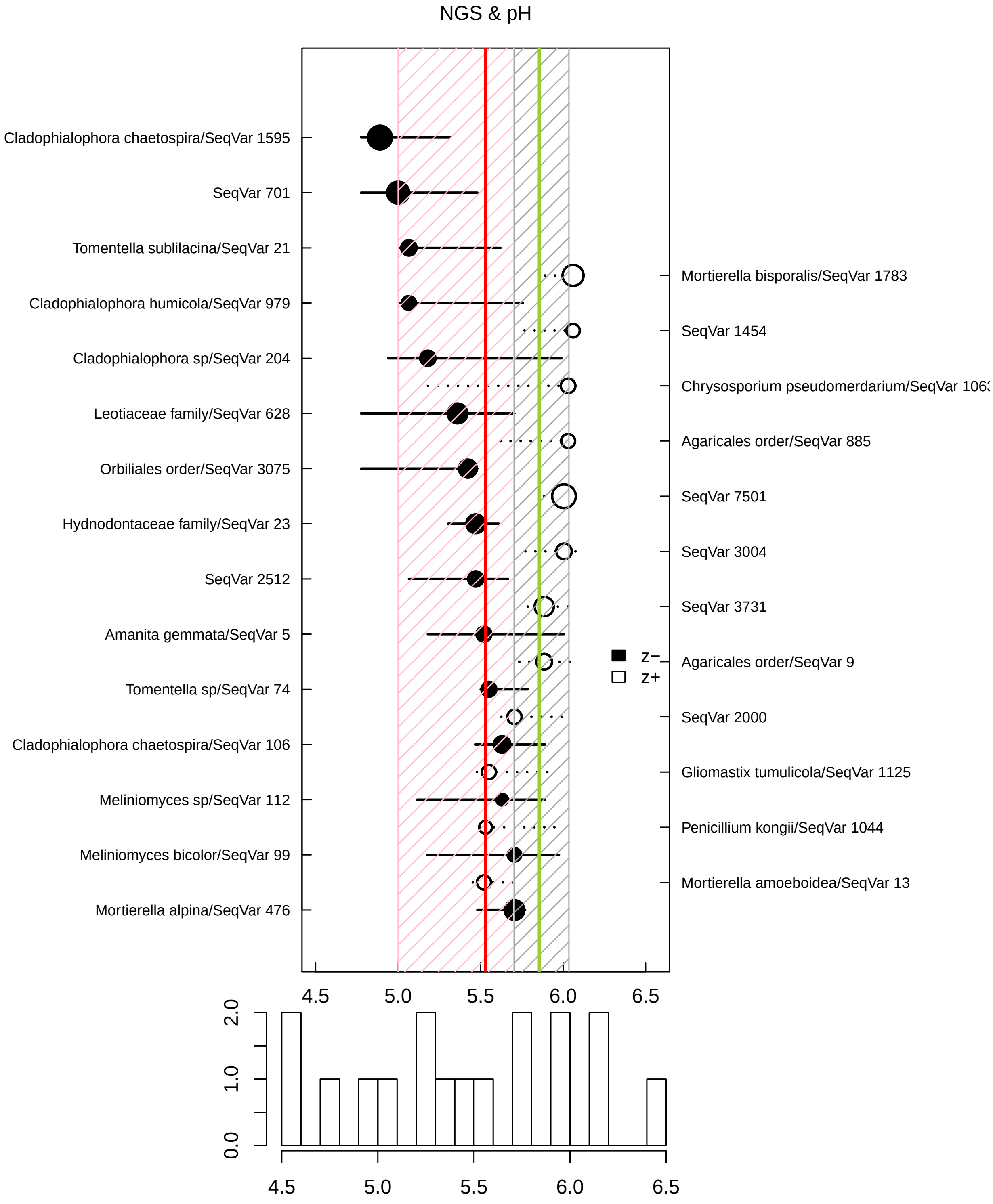

Figure C.11: NGS data TITAN results for pH.

**Carbon to Nitrogen Ratio:** Negative (z-) indicator taxa suggest a synchronous change-point at approximately 17 C:N (Median filtered sum(z-) was 17.947). Positive (z+) indicator taxa have asynchronous changes over the environmental gradient (median filtered sum(z+) was 26.967). The widely distributed changes in z+ indicator taxa together span most of the range of the C:N gradient. This suggests a gradual addition of taxa tolerant of high C:N values, instead of an ecological community threshold.

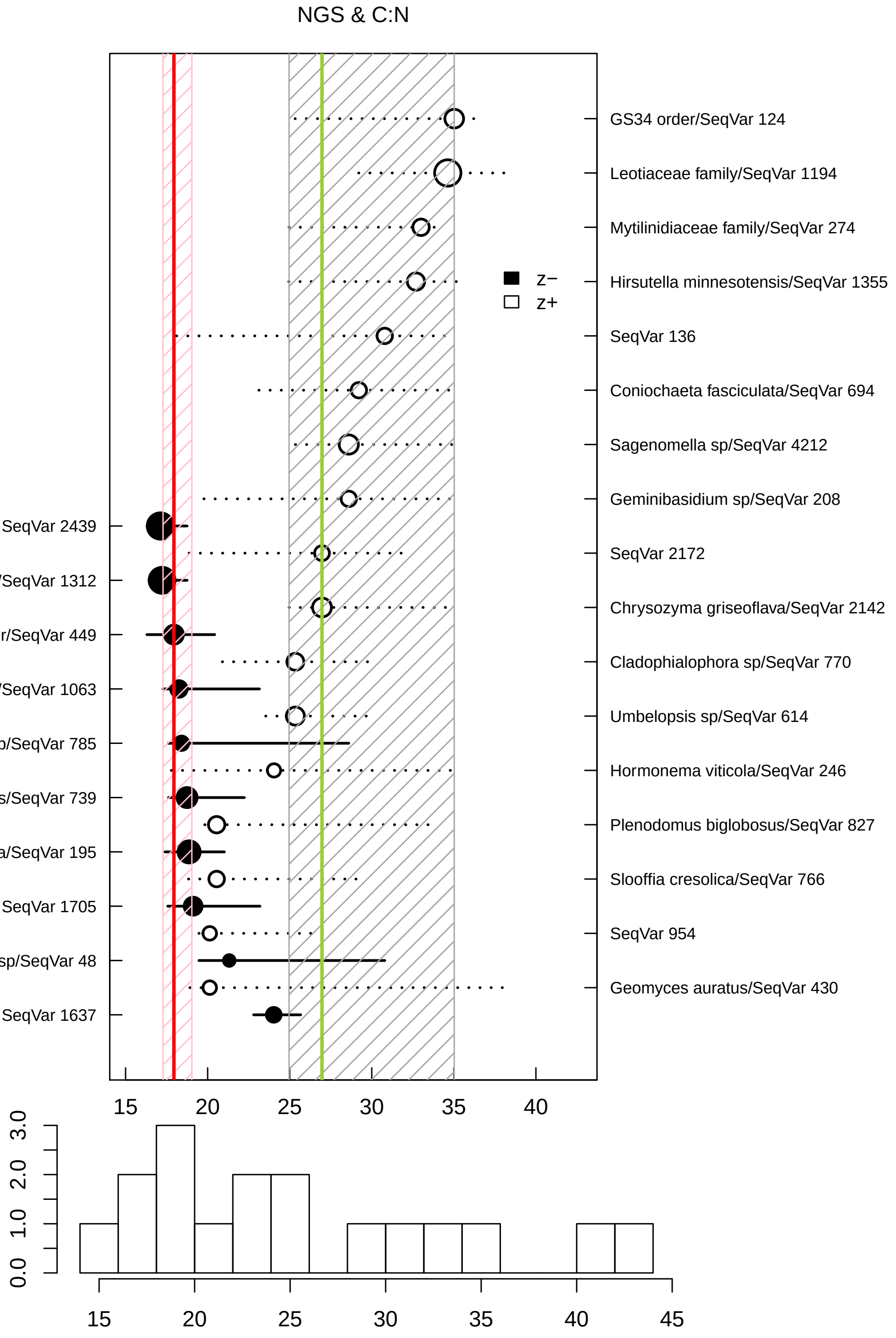

Figure C.12: NGS data TITAN results for carbon to nitrogen ratio.

**% C:** There are more SVs associated with lower (z-) than higher (z+) % C in the NGS dataset. While negative indicator taxa exhibit a synchronous change-point at approximately 4-5 % C the pattern for z+ taxa is not clear (median filtered sum(z-) = 4.682; median filtered sum(z+) = 6.55). This synchronous change is consistent with an ecological community threshold. Results for the collections dataset was ambiguous, with only a few pure and reliable taxa associated with higher (z+) %C.

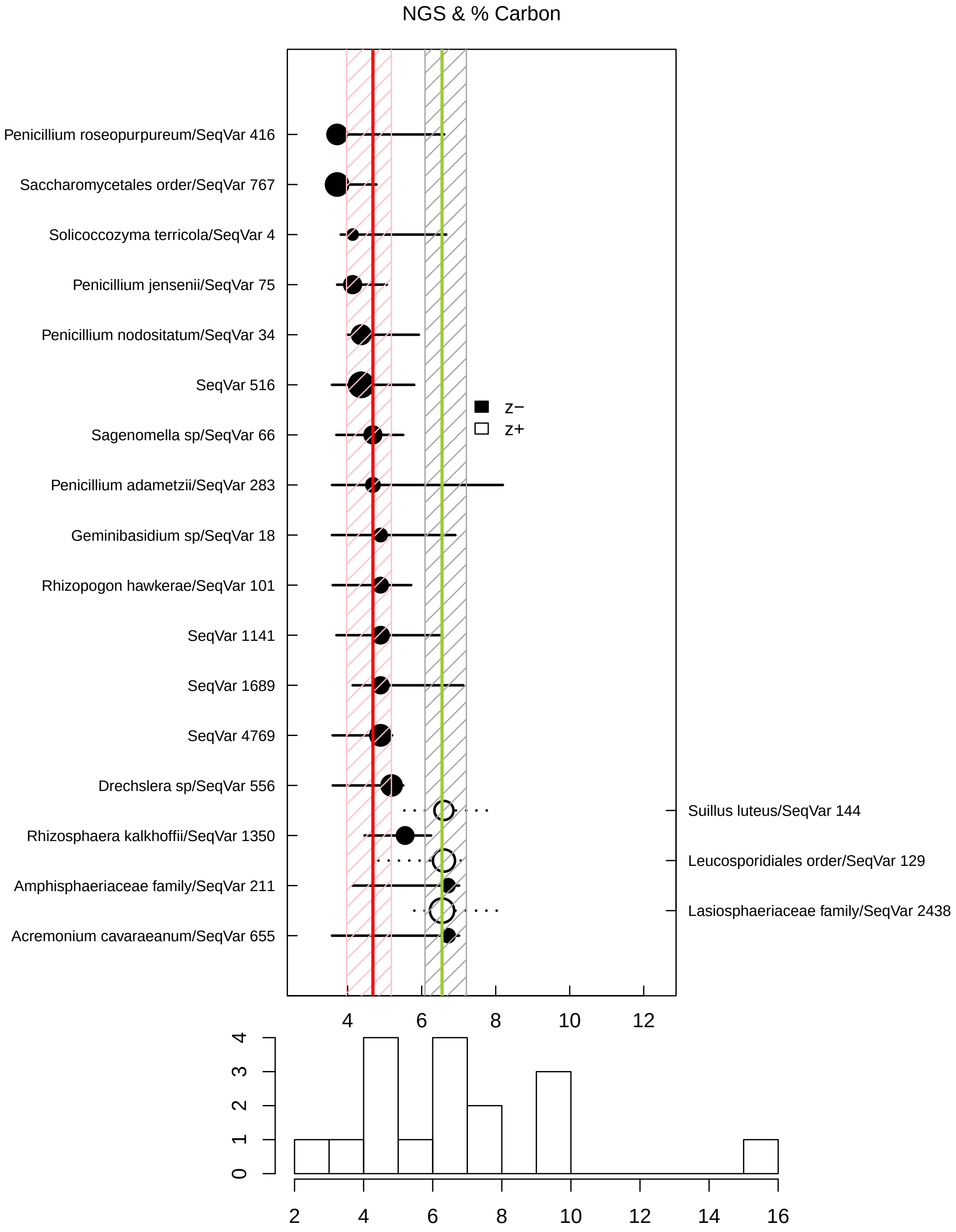

Figure C.13: NGS data TITAN results for percent carbon.

**Percent N:** there are more SVs associated with lower (z-) than higher (z+) % N in the NGS dataset. At approximately 0.2% N, there is evidence of synchronous change-points for z- indicator taxa, suggesting an ecological community threshold. However, as with % C the z+ taxa are added gradually to the community as % N increases (median filtered sum(z-) = 0.22; median filtered sum(z+) = 0.321). Results for the collections dataset suggest a community threshold for z+ taxa between 0.3-0.4% N, while results for z- taxa are ambiguous.

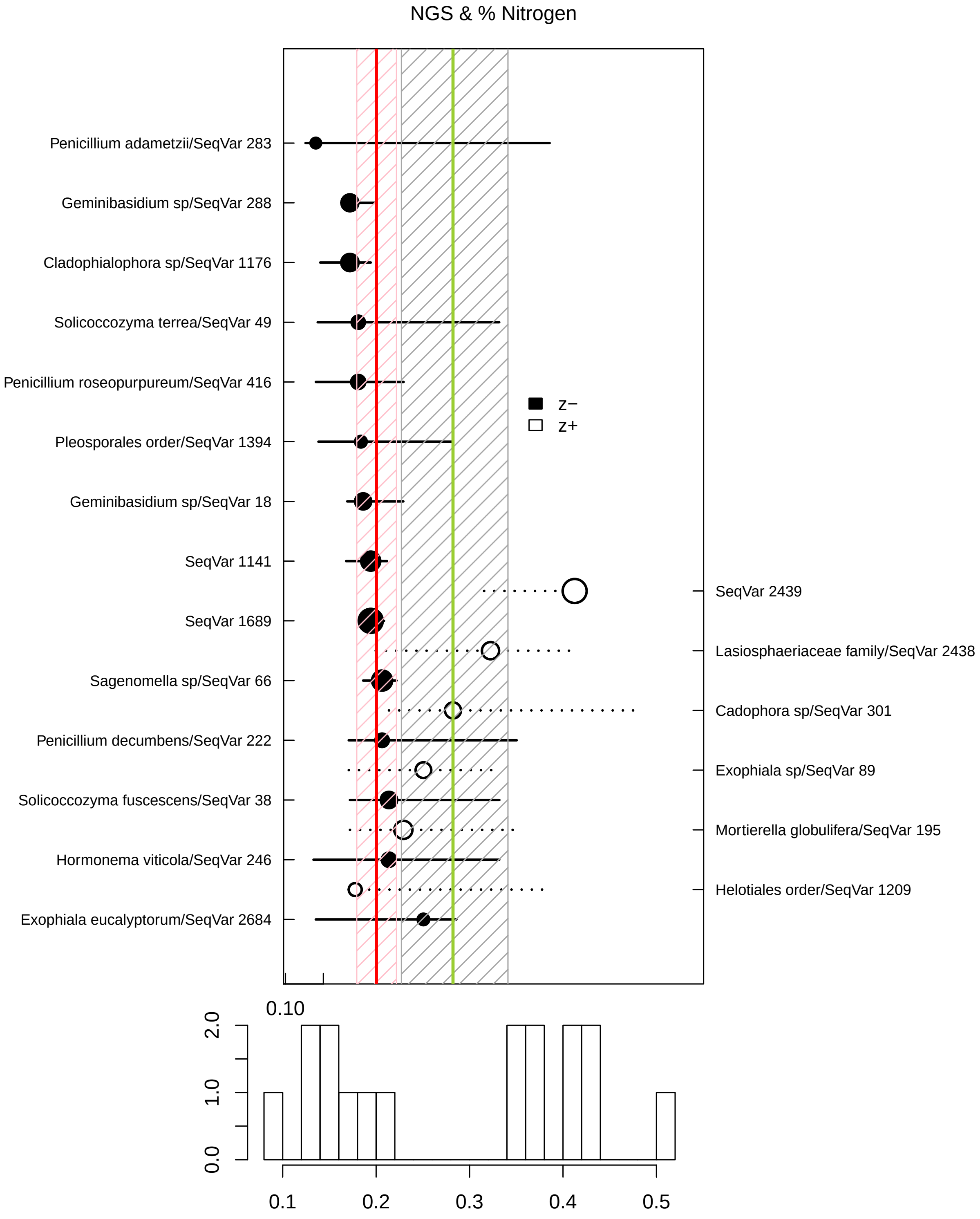

Figure C.14: NGS data TITAN results for percent nitrogen.

## C.6 Tree and shrub community preference in mushroom collection dataset

In the collections dataset, multiple fungal genera exhibited preferences for the native or ornamental tree and shrub community groups. These are presented below with annotations about the genera.

| Genus | Species | Vegetation Type | Mean Statistic | Trophic Mode | Notes |
|---|---|---|---|---|---|
| Marasmiellus | tricolor | Native Shrub | 0.500 | Saprotroph | Marasmiellus spp are closely related to Gymnopus spp. They are saprobic, M. tricolor reported on grass in Europe but in the US also on conifers; the genus generally is found on small woody debris of conifers and hardwoods [@henrici2016; @mushroomexpert]. |
| Boletus | edulis;<br>fibrillosus | Ornamental Shrub | 0.535 | Symbiotroph | Boletus spp are ectomycorrhizal and commonly associated with conifer trees, including Pinus. They are common in both forests and urban ecosystems where ectomycorrhizal trees are present [@mushroomexpert]. |
| Steccherinum | ochraceum | Ornamental Shrub | 0.535 | Saprotroph | Steccherinum spp are toothed mushrooms saprobic on the deadwood of hardwood trees. Grows gregariously on sticks, logs, or stumps and causes white rot [@mushroomexpert]. |
| Gymnopus | luxurians;<br>peronatus;<br>villosipes | Native Tree | 0.620 | Saprotroph | Gymnopus spp are saprobic, frequently growing in leaf/needle litter and wood chips. Gymnopus villosipes is frequently found clustered under conifers and fruiting on conifer litter, while G. peronatus and G. luxurians appear to grow on both hardwoods and conifers [@mushroomexpert; @mykoweb]. In the Puget Trough they are mainly litter decomposers. |
| Lycoperdon | perlatum;<br>pyriforme;<br>subumbrinum | Native Tree | 0.600 | Saprotroph | Lycoperdon spp are saprobic woodland puffballs that grow under both hardwoods and conifers. Some species grow on wood (incl. L. pyriforme), though most are found in soil [@mushroomexpert]. L. perlatum is widespread, while L. subumbrinum is a relatively new species from Europe found in deciduous forests. |

| | | | | | |
|---|---|---|---|---|---|
| Arrhenia | acerosa | Native Tree | 0.577 | Saprotroph, Pathotroph | Arrhenia spp are bryophilic (grows on mosses) and known from European collections. Little ecological info? |
| Marasmiellus | tricolor | Native Tree | 0.500 | Saprotroph | Marasmiellus spp are closely related to Gymnopus spp. They are saprobic, M. tricolor reported on grass in Europe but in the US also on conifers; the genus generally is found on small woody debris of conifers and hardwoods [@henrici2016; @mushroomexpert]. |
| Cyclocybe | erebia | Ornamental Deciduous Tree | 0.535 | Saprotroph | Cyclocybe spp are saprobic and often associated with decaying hardwood and conifer debris and leaf litter. Cyclocybe is found in mulch, bare soil, leaf litter, and along the edge of forests and forest tracks [@hermanson1986]. |

## C.7 Landscape and management category preference in NGS and specimen datasets with annotations

### C.7.1 For specimen collections:

| Genus | Species | Gradient | Mean Statistic | Trophic Mode | Ecology Notes |
|---|---|---|---|---|---|
| Amanita | aprica;<br>breckonii;<br>gemmata;<br>muscaria;<br>pantherina | Yes Stands Predate | 0.577 | Symbiotroph, Saprotroph | Amanita are generalist mycorrhizal fungi. The genus occupies a wide geographic and ecological niche [@geml2008]. Amanita is common in the Pacific Northwest; it is mycorrhizal with both conifers and hardwoods [@mushroomexpert]. Various Amanita species found in association with Douglas fir, madrone, and oak among others; found in conifer and mixed forests. |
| Arrhenia | acerosa | Yes Stands Predate | 0.542 | Saprotroph, Pathotroph | Arrhenia are bryophilic (grow on mosses) saprotrophs known from European collections. They are common in the arctic and subarctic [@ohenoja2010]. Preference for sites with stands predating development suggests these sites have greater moss abundance [unsupported]. |
| Clitocybe | metachroa;<br>nebularis | Yes Stands Predate | 0.612 | Saprotroph, Pathotroph | Clitocybe sp. are saprotrophic and pathotrophic fungi. As saprotrophs, they prefer partly decomposed leaves to freshly fallen leaves, and selectively remove lignin and enhance nitrogen mineralization [@osono2011]. |
| Cyclocybe | erebia | No Stands Predate | 0.577 | Saprotroph | Cyclocybe sp. (also Agrocybe) are saprotrophic fungi frequently growing on stumps, decaying hardwoods, leaf litter, humus, and bare soil. They are found in fields, grasslands, and open woods and are adaptable to urban areas, and are found in lawns and roadsides [@hermanson1986]. |
| Strobilurus | trullisatus | Yes Stands Predate | 0.609 | Saprotroph | Strobilurus is a saprotrophic genus, species of which grow on fallen pinecones [@redhead1980]. |

| | | | | | |
|---|---|---|---|---|---|
| Trametes | gibbosum; versicolor | Yes Stands Predate | 0.570 | Saprotroph | Trametes sp. are saprobic on hardwoods and conifers. In the Pacific Northwest, various Trametes species have long been acknowledged to cause decay in Douglas fir and other conifers [@boyce1930]. |
| Xerocomellus | cisalpinus; zelleri | Yes Stands Predate | 0.612 | Symbiotroph | Xerocomellus are saprotrophic. In the Pacific Northwest, species in the genus are found on the ground near or on decaying wood of hemlock, cedar, alder, spruce, and fir; more generally in conifer but also mixed forests [@scates1982]. |

### C.7.2 For NGS fungi

| Taxonomy | Gradient | Mean Statistic | Trophic Mode | Ecology Notes |
|---|---|---:|---|---|
| Leucosporidiales order | Yes stands predate | 0.543 | NA | This sequence variant is a member of Leucosporidiales, an order of mycoparasitic fungi. |
| Umbelopsis sp | Yes stands predate | 0.542 | Saprotroph, Symbiotroph | Members of the genus Umbelopsis are saprotrophic and symbiotrophic, with many lipid producing species [@takeda2014]. The genus is frequently isolated from soil and leaf litter samples, and has been found on Abies and Betula leaf litter [@osono2007]. The genus is a widespread generalist mycorrhizal taxa, found on Quercus, Acer, Liriodendron, and Picea roots; in eastern Washington the genus was identified on Pinus ponderosa and Pseudotsuga menziesii roots. Umbelopsis are physiologically well suited to disturbed sites and nutrient poor environments, including burned harvest stands, which may account for their preference for unmanaged forests [@vandegrift2007]. |
| Wilcoxina rehmii | Yes stands predate | 0.574 | Symbiotroph | Wilcoxina rehmii is an ectomycorrhizal species frequently found on Douglas fir (Pseudotsuga menziesii) roots [@bingham2012]. |
| Coniochaeta mutabilis | Yes stands predate | 0.569 | Pathotroph, Saprotroph, Symbiotroph | Coniochaeta mutabilis is part of a genus of generalist saprotrophs, endophites (possibly symbiotrophic), and pathotrophs. C. mutabilis specifically is implicated as a human pathogen involved in peritonitis and sepsis [@damm2010]. The species is also known to colonize Douglas-fir damaged by commercial thinning [@kiser2010]. |

## C.8 Comparison table of taxa found in NGS and collections datasets

This table identifies which genus are found in both datasets, which are found only in the NGS soil observations, and which were only observed as mushrooms collected on site.

| Taxa | Genus found in both datasets | Genus found only via NGS | Genus found only via collections |
|---|---|---|---|
| Abortiporus | | | Y |
| Abrothallus | | Y | |
| Acanthobasidium | | Y | |
| Acanthostigma | | Y | |
| Acaulospora | | Y | |
| Acidomelania | | Y | |
| Acidothrix | | Y | |
| Acremoniopsis | | Y | |
| Acremonium | | Y | |
| Acrostalagmus | | Y | |
| Agaricus | Y | | |
| Agrocybe | Y | | |
| Alatosessilispora | | Y | |
| Alatospora | | Y | |
| Aleuria | Y | | |
| Aleurodiscus | | | Y |
| Allantophomopsis | | Y | |
| Alpinaria | | Y | |
| Alpova | | Y | |
| Alternaria | | Y | |
| Amanita | Y | | |
| Amaurodon | | Y | |

| | | |
|---|---|---|
| Ambispora | | Y |
| Amorphotheca | | Y |
| Amphinema | | Y |
| Ampulloclitocybe | | Y |
| Angustimassarina | | Y |
| Antarctomyces | | Y |
| Aphanoascus | | Y |
| Apiognomonia | | Y |
| Apiosordaria | | Y |
| Apiotrichum | | Y |
| Apodus | | Y |
| Aquapeziza | | Y |
| Arachnopeziza | | Y |
| Arbusculina | | Y |
| Archaeorhizomyces | | Y |
| Archaeospora | | Y |
| Armillaria | Y | |
| Arrhenia | Y | |
| Arthonia | | Y |
| Arthopyrenia | | Y |
| Arthrobotrys | | Y |
| Arthrocladium | | Y |
| Arthroderma | | Y |
| Arthrographis | | Y |
| Arthropsis | | Y |
| Articulospora | | Y |
| Ascobolus | | Y |
| Ascochyta | | Y |
| Aspergillus | | Y |
| Athelia | | Y |
| Athelopsis | | Y |

| | | | |
|---|---|---|---|
| Atractospora | | Y | |
| Aureobasidium | | Y | |
| Auricularia | | Y | |
| Auriscalpium | | | Y |
| Auxarthron | | Y | |
| Basidioascus | | Y | |
| Basidiobolus | | Y | |
| Basidiodendron | | Y | |
| Bauerago | | Y | |
| Bjerkandera | | | Y |
| Blastocladiella | | Y | |
| Bolbitius | | | Y |
| Boletus | Y | | |
| Botryobasidium | | Y | |
| Botryosphaeria | | Y | |
| Botrytis | | Y | |
| Bovista | | | Y |
| Bradymyces | | Y | |
| Brevicellicium | | Y | |
| Buckleyzyma | | Y | |
| Byssocorticium | | Y | |
| Byssonectria | | Y | |
| Cadophora | | Y | |
| Calcarisporiella | | Y | |
| Calcarisporium | | Y | |
| Callistosporium | Y | | |
| Calocera | Y | | |
| Calvulinopsis | | | Y |
| Calycina | | Y | |
| Calyptrozyma | | Y | |
| Camarophyllopsis | | Y | |

| | | | |
|---|---|---|---|
| Candelaria | | Y | |
| Candelariella | | Y | |
| Candida | | Y | |
| Cantharellus | | | Y |
| Capnobotryella | | Y | |
| Capronia | | Y | |
| Catenulostroma | | Y | |
| Cenococcum | | Y | |
| Cephaliophora | | Y | |
| Ceratobasidium | | Y | |
| Ceratocystis | | Y | |
| Cercophora | | Y | |
| Cerinosterus | | Y | |
| Cetraspora | | Y | |
| Chaetomium | | Y | |
| Chaetosphaeria | | Y | |
| Chaetosphaeronema | | Y | |
| Chalara | | Y | |
| Chalciporus | Y | | |
| Chlamydotubeufia | | Y | |
| Chlorophyllum | | Y | |
| Chondrostereum | | | Y |
| Chrysosporium | | Y | |
| Chrysozyma | | Y | |
| Cistella | | Y | |
| Cladophialophora | | Y | |
| Cladorrhinum | | Y | |
| Cladosporium | | Y | |
| Claroideoglomus | | Y | |
| Clavaria | Y | | |
| Clavatospora | | Y | |

| | | | |
|---|---|---|---|
| Clavulina | Y | | |
| Clavulinopsis | Y | | |
| Clitocella | | Y | |
| Clitocybe | Y | | |
| Clitopilus | Y | | |
| Clonostachys | | Y | |
| Clypeosphaeria | | Y | |
| Colacogloea | | Y | |
| Coleophoma | | Y | |
| Collarina | | Y | |
| Collophora | | Y | |
| Colpoma | | Y | |
| Coniochaeta | | Y | |
| Coniophora | | Y | |
| Conioscypha | | Y | |
| Coniothyrium | | Y | |
| Conlarium | | Y | |
| Conocybe | Y | | |
| Coprinellus | Y | | |
| Coprinopsis | Y | | |
| Coprinus | Y | | |
| Copronopsis | | | Y |
| Cordyceps | | Y | |
| Coronatomyces | | Y | |
| Cortinarius | Y | | |
| Cosmospora | | Y | |
| Cotylidia | | Y | |
| Crepidotus | | | Y |
| Crocicreas | | Y | |
| Crucibulum | | | Y |
| Cryptococcus | | Y | |

| | | | |
|---|---|---|---|
| Cryptosporiopsis | | Y | |
| Cryptotrichosporon | | Y | |
| Cudoniella | | Y | |
| Cuniculitrema | | Y | |
| Cuphophyllus | | Y | |
| Curvibasidium | | Y | |
| Curvularia | | Y | |
| Cutaneotrichosporon | | Y | |
| Cyathus | Y | | |
| Cyclocybe | | | Y |
| Cylindrocladiella | | Y | |
| Cylindrosympodium | | Y | |
| Cyphellophora | | Y | |
| Cyphellostereum | | | Y |
| Cystobasidium | | Y | |
| Cystodendron | | Y | |
| Cystofilobasidium | | Y | |
| Dacrymyces | | | Y |
| Dacryopinax | | Y | |
| Dactylaria | | Y | |
| Dactylellina | | Y | |
| Dactylonectria | | Y | |
| Deconica | | | Y |
| Delicatula | | Y | |
| Devriesia | | Y | |
| Diaporthe | | Y | |
| Dichostereum | | Y | |
| Dictyosporium | | Y | |
| Didymella | | Y | |
| Dioszegia | | Y | |
| Dipodascus | | Y | |

| | | | |
|---|---|---|---|
| Diversispora | | Y | |
| Dominikia | | Y | |
| Dothiora | | Y | |
| Dothiorella | | Y | |
| Drechslera | | Y | |
| Elaphomyces | | Y | |
| Endogone | | Y | |
| Endophoma | | Y | |
| Entoloma | Y | | |
| Entorrhiza | | Y | |
| Entrophospora | | Y | |
| Eocronartium | | Y | |
| Epicoccum | | Y | |
| Erythrobasidium | | Y | |
| Eucasphaeria | | Y | |
| Evernia | | Y | |
| Exophiala | | Y | |
| Fayodia | | Y | |
| Fayoidia | | | Y |
| Fellozyma | | Y | |
| Fenestella | | Y | |
| Fibroporia | | Y | |
| Fibulochlamys | | Y | |
| Filobasidium | | Y | |
| Flagelloscypha | | Y | |
| Flagellospora | | Y | |
| Flammula | | | Y |
| Flammulina | | | Y |
| Fomitopsis | | | Y |
| Fonsecazyma | | Y | |
| Funneliformis | | Y | |

| | | | |
|---|---|---|---|
| Fusarium | | Y | |
| Fusicolla | | Y | |
| Fusidium | | Y | |
| Galerina | Y | | |
| Gamsylella | | Y | |
| Gamundia | | Y | |
| Ganoderma | Y | | |
| Geastrum | | Y | |
| Geminibasidium | | Y | |
| Gemmina | | Y | |
| Genea | | Y | |
| Genolevuria | | Y | |
| Geoglossum | | Y | |
| Geomyces | | Y | |
| Geopora | | Y | |
| Geopyxis | | Y | |
| Geotrichum | | Y | |
| Gerhardtia | | Y | |
| Gibberella | | Y | |
| Gibellulopsis | | Y | |
| Glarea | | Y | |
| Gleophyllum | | | Y |
| Gliomastix | | Y | |
| Gliophorus | | Y | |
| Gloeohypochnicium | | Y | |
| Glomus | | Y | |
| Gomphidius | Y | | |
| Gorgomyces | | Y | |
| Guehomyces | | Y | |
| Gymnopus | Y | | |
| Gyoerffyella | | Y | |

| | | | |
|---|---|---|---|
| Gyromitra | | | Y |
| Halokirschsteiniothelia | | Y | |
| Hamamotoa | | Y | |
| Hamatocanthoscypha | | Y | |
| Hamigera | | Y | |
| Haptocillium | | Y | |
| Hebeloma | Y | | |
| Helgardia | | Y | |
| Helicodendron | | Y | |
| Helicoma | | Y | |
| Helicosporium | | Y | |
| Helvella | Y | | |
| Hemibeltrania | | Y | |
| Hemimycena | | | Y |
| Henningsomyces | | Y | |
| Herpotrichia | | Y | |
| Heterobasidion | | Y | |
| Heterocephalacria | | Y | |
| Heterosphaeria | | Y | |
| Hirsutella | | Y | |
| Hohenbuehelia | Y | | |
| Holtermanniella | | Y | |
| Hormonema | | Y | |
| Humicola | | Y | |
| Hyalopeziza | | Y | |
| Hyalorbilia | | Y | |
| Hyaloscypha | | Y | |
| Hydnomerulius | | Y | |
| Hydnotrya | | Y | |
| Hygrocybe | Y | | |
| Hygrophoropsis | | | Y |

| | | | |
|---|---|---|---|
| Hygrophorus | Y | | |
| Hymenogaster | | Y | |
| Hymenoscyphus | | Y | |
| Hyphodiscus | | Y | |
| Hyphodontia | | Y | |
| Hyphodontiella | | Y | |
| Hypholoma | Y | | |
| Hypochnicium | | Y | |
| Hypomyces | Y | | |
| Idriella | | Y | |
| Ilyonectria | | Y | |
| Immersidiscosia | | Y | |
| Infundichalara | | Y | |
| Inocybe | Y | | |
| Ionomidotis | | Y | |
| Itersonilia | | Y | |
| Jaapia | | Y | |
| Kabatiella | | Y | |
| Kavinia | | Y | |
| Knufia | | Y | |
| Kockovaella | | Y | |
| Krasilnikovozyma | | Y | |
| Kriegeria | | Y | |
| Laccaria | Y | | |
| Lachnum | | Y | |
| Lactarius | Y | | |
| Lambertella | | Y | |
| Lapidomyces | | Y | |
| Lecanicillium | | Y | |
| Leccinum | | | Y |
| Lecophagus | | Y | |

| | | | |
|---|---|---|---|
| Leohumicola | | Y | |
| Lepiota | Y | | |
| Lepista | Y | | |
| Leptodiscella | | Y | |
| Leptodontidium | | Y | |
| Leptonia | | | Y |
| Leptosphaeria | | Y | |
| Leratiomyces | Y | | |
| Leucangium | | Y | |
| Leucoagaricus | Y | | |
| Leucocoprinus | | | Y |
| Leucogyrophana | | Y | |
| Leuconeurospora | | Y | |
| Leucopaxillus | Y | | |
| Leucosporidium | | Y | |
| Lindtneria | | Y | |
| Lipomyces | | Y | |
| Lirula | | Y | |
| Lophiostoma | | Y | |
| Lophiotrema | | Y | |
| Lophium | | Y | |
| Lophodermium | | Y | |
| Lulwoana | | Y | |
| Lycoperdon | Y | | |
| Lyophyllum | Y | | |
| Maasoglossum | | Y | |
| Macrocystidia | | | Y |
| Marasmiellus | Y | | |
| Marasmius | Y | | |
| Mariannaea | | Y | |
| Marssonina | | Y | |

| | | | |
|---|---|---|---|
| Mastigobasidium | | Y | |
| Melanelixia | | Y | |
| Melanochaeta | | Y | |
| Melanogaster | | Y | |
| Melanoleuca | | | Y |
| Melanospora | | Y | |
| Meliniomyces | | Y | |
| Membranomyces | | Y | |
| Meruliopsis | | | Y |
| Metacordyceps | | Y | |
| Metarhizium | | Y | |
| Meyerozyma | | Y | |
| Micarea | | Y | |
| Microbotryum | | Y | |
| Microdochium | | Y | |
| Micromphale | | | Y |
| Microscypha | | Y | |
| Microsporomyces | | Y | |
| Minimedusa | | Y | |
| Minimelanolocus | | Y | |
| Minutisphaera | | Y | |
| Mollisia | | Y | |
| Monographella | | Y | |
| Morganella | | | Y |
| Mortierella | | Y | |
| Mucor | | Y | |
| Mycena | Y | | |
| Mycenella | Y | | |
| Mycetinis | | | Y |
| Mycoarthris | | Y | |
| Mycoleptodiscus | | Y | |

| | | | |
|---|---|---|---|
| Mycosphaerella | | Y | |
| Myriodontium | | Y | |
| Myrmecridium | | Y | |
| Myrothecium | | Y | |
| Myxocephala | | Y | |
| Nadsonia | | Y | |
| Naematelia | | Y | |
| Naganishia | | Y | |
| Naucoria | Y | | |
| Nectria | | Y | |
| Nectriopsis | | Y | |
| Nematoctonus | | Y | |
| Neoascochyta | | Y | |
| Neobulgaria | | Y | |
| Neocatenulostroma | | Y | |
| Neodevriesia | | Y | |
| Neonectria | | Y | |
| Neophaeococcomyces | | Y | |
| Neophaeosphaeria | | Y | |
| Neosartorya | | Y | |
| Neosetophoma | | Y | |
| Neostagonospora | | Y | |
| Nidula | Y | | |
| Nidularia | | | Y |
| Nidulariopsis | | Y | |
| Nolanea | | | Y |
| Oberwinklerozyma | | Y | |
| Occultifur | | Y | |
| Ochroconis | | Y | |
| Odontia | | Y | |
| Ogataea | | Y | |

| | | | |
|---|---|---|---|
| Oidiodendron | | Y | |
| Oligoporus | | | Y |
| Oliveonia | | Y | |
| Olpidium | | Y | |
| Omphalina | | | Y |
| Ophiosphaerella | | Y | |
| Orbilia | | Y | |
| Otidea | | Y | |
| Oxyporus | | | Y |
| Pachyomphalina | | | Y |
| Pachyphlodes | | Y | |
| Palaeospora | | Y | |
| Panaeolina | | | Y |
| Panaeolus | Y | | |
| Papiliotrema | | Y | |
| Paraboeremia | | Y | |
| Paraconiothyrium | | Y | |
| Paraglomus | | Y | |
| Paralepista | | Y | |
| Paramicrosporidium | | Y | |
| Paraphaeosphaeria | | Y | |
| Paraphoma | | Y | |
| Parasola | Y | | |
| Parastagonospora | | Y | |
| Paratritirachium | | Y | |
| Parmelia | | Y | |
| Paxillus | Y | | |
| Penicillium | | Y | |
| Penidiella | | Y | |
| Peniophora | | Y | |
| Periconia | | Y | |

| | | | |
|---|---|---|---|
| Perusta | | Y | |
| Pestalotiopsis | | Y | |
| Peterozyma | | Y | |
| Pezicula | | Y | |
| Peziza | | Y | |
| Pezoloma | | Y | |
| Phacidium | | Y | |
| Phaeoacremonium | | Y | |
| Phaeococcomyces | | Y | |
| Phaeolus | Y | | |
| Phaeophyscia | | Y | |
| Phaeosphaeria | | Y | |
| Phaeotremella | | Y | |
| Phanerochaete | | | Y |
| Phialocephala | | Y | |
| Phialophora | | Y | |
| Phlebia | | | Y |
| Phlebiella | | Y | |
| Pholiota | Y | | |
| Pholiotina | | | Y |
| Phomatospora | | Y | |
| Pichia | | Y | |
| Pilidium | | Y | |
| Piloderma | Y | | |
| Piskurozyma | | Y | |
| Plagiostoma | | Y | |
| Plectania | Y | | |
| Plectosphaerella | | Y | |
| Plenodomus | | Y | |
| Pleurophoma | | Y | |
| Pleurostoma | | Y | |

| | | | |
|---|---|---|---|
| Pleurotheciella | | Y | |
| Pluteus | | Y | |
| Pochonia | | Y | |
| Podonectria | | Y | |
| Podospora | | Y | |
| Polycauliona | | Y | |
| Postia | Y | | |
| Preussia | | Y | |
| Psathyrella | Y | | |
| Pseudaleuria | | Y | |
| Pseudallescheria | | Y | |
| Pseudeurotium | | Y | |
| Pseudoclathrosphaerina | | Y | |
| Pseudocoleophoma | | Y | |
| Pseudogymnoascus | | Y | |
| Pseudohydnum | | | Y |
| Pseudohyphozyma | | Y | |
| Pseudolachnella | | Y | |
| Pseudopithomyces | | Y | |
| Pseudorobillarda | | Y | |
| Pseudosigmoidea | | Y | |
| Pseudotomentella | | Y | |
| Psilocybe | Y | | |
| Pulvinula | | Y | |
| Pustularia | | Y | |
| Pyrenochaeta | | Y | |
| Pyrenochaetopsis | | Y | |
| Ramaria | Y | | |
| Ramariopsis | | Y | |
| Ramicandelaber | | Y | |
| Ramularia | | Y | |

| | | | |
|---|---|---|---|
| Rasamsonia | | Y | |
| Rectipilus | | Y | |
| Retiarius | | Y | |
| Rhinocladiella | | Y | |
| Rhizophagus | | Y | |
| Rhizopogon | Y | | |
| Rhizoscyphus | | Y | |
| Rhizosphaera | | Y | |
| Rhodocybe | | Y | |
| Rhodophana | | | Y |
| Rhodosporidiobolus | | Y | |
| Rhodotorula | | Y | |
| Rickenella | Y | | |
| Roesleria | | Y | |
| Rosellinia | | Y | |
| Rubellisphaeria | | Y | |
| Russula | Y | | |
| Rutsroemia | | | Y |
| Rutstroemia | | | Y |
| Saccharicola | | Y | |
| Sagenomella | | Y | |
| Saitozyma | | Y | |
| Sakaguchia | | Y | |
| Sampaiozyma | | Y | |
| Sarcinomyces | | Y | |
| Sarocladium | | Y | |
| Savoryella | | Y | |
| Scedosporium | | Y | |
| Schizophyllum | | | Y |
| Schizothecium | | Y | |
| Schwanniomyces | | Y | |

| | | | |
|---|---|---|---|
| Scleroconidioma | | Y | |
| Scleroderma | Y | | |
| Scleropezicula | | Y | |
| Sclerostagonospora | | Y | |
| Scolecobasidium | | Y | |
| Scoliciosporum | | Y | |
| Scopuloides | | Y | |
| Scutellinia | | Y | |
| Scutellospora | | Y | |
| Scytalidium | | Y | |
| Sebacina | | Y | |
| Seiridium | | Y | |
| Sepedonium | | Y | |
| Septobasidium | | Y | |
| Septoglomus | | Y | |
| Septoriella | | Y | |
| Serendipita | | Y | |
| Setomelanomma | | Y | |
| Setophoma | | Y | |
| Simocybe | | Y | |
| Simplicillium | | Y | |
| Sistotrema | | Y | |
| Sistotremastrum | | Y | |
| Slooffia | | Y | |
| Slopeiomyces | | Y | |
| Solheimia | | Y | |
| Solicoccozyma | | Y | |
| Sordaria | | Y | |
| Sphaerobolus | | | Y |
| Sphaerosporella | | Y | |
| Spinellus | | | Y |

| | | | |
|---|---|---|---|
| Spiromastix | | Y | |
| Spiromyces | | Y | |
| Spirosphaera | | Y | |
| Sporobolomyces | | Y | |
| Steccherinum | | | Y |
| Stereum | | | Y |
| Strelitziana | | Y | |
| Strobilurus | | | Y |
| Stropharia | | | Y |
| Subulicystidium | | Y | |
| Sugitazyma | | Y | |
| Sugiyamaella | | Y | |
| Suillus | Y | | |
| Sydowia | | Y | |
| Symmetrospora | | Y | |
| Sympodiella | | Y | |
| Syzygospora | | Y | |
| Talaromyces | | Y | |
| Taphrina | | Y | |
| Tapinella | | | Y |
| Tarzetta | | | Y |
| Teichospora | | Y | |
| Telamonia | | | Y |
| Tetrachaetum | | Y | |
| Tetracladium | | Y | |
| Tetragoniomyces | | Y | |
| Thanatephorus | | Y | |
| Thelephora | Y | | |
| Thelonectria | | Y | |
| Thermoascus | | Y | |
| Thielaviopsis | | Y | |

| | | | |
|---|---|---|---|
| Tolypocladium | | Y | |
| Tomentella | | Y | |
| Tomentellopsis | | Y | |
| Trametes | | | Y |
| Trechispora | | Y | |
| Tremella | Y | | |
| Tremellodendron | | | Y |
| Trichaptum | | | Y |
| Trichocladium | | Y | |
| Trichoderma | | Y | |
| Tricholoma | Y | | |
| Tricholomopsis | | Y | |
| Trichomerium | | Y | |
| Trichophaea | | Y | |
| Trichophaeopsis | | Y | |
| Trichosporon | | Y | |
| Trichothecium | | Y | |
| Tricladium | | Y | |
| Trimmatostroma | | Y | |
| Tritirachium | | Y | |
| Tubaria | Y | | |
| Tuber | | Y | |
| Tubulicrinis | | Y | |
| Tylospora | | Y | |
| Tyromyces | | | Y |
| Udeniomyces | | Y | |
| Umbelopsis | | Y | |
| Unguicularia | | Y | |
| Valsa | | Y | |
| Valsonectria | | Y | |
| Vascellum | | | Y |

| | | | |
|---|---|---|---|
| Venturia | | Y | |
| Venturiocistella | | Y | |
| Vermispora | | Y | |
| Veronaeopsis | | Y | |
| Verticillium | | Y | |
| Volutella | | Y | |
| Volvariella | | Y | |
| Westerdykella | | Y | |
| Wilcoxina | | Y | |
| Xenopolyscytalum | | Y | |
| Xerocomellus | Y | | |
| Xerocomus | | Y | |
| Xeromphalina | | | Y |
| Xylaria | | | Y |
| Yurkovia | | Y | |
| Zalerion | | Y | |
| Zopfiella | | Y | |
| Zygorhynchus | | Y | |