Impacts of Amur Honeysuckle (*Lonicera maackii*) Removal on the Composition of Avian Assemblages in Rural Riparian Forests

Thesis

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Abstract

Amur honeysuckle (*Lonicera maackii*) was introduced to North America in the late 1880s and has since become highly invasive throughout the midwestern and northeastern United States. Amur honeysuckle-dominated habitat can be detrimental to wildlife including birds. The invasive shrub attracts generalist avian species and represents an ecological trap where manipulative habitat signals have been shown to negatively influence avian populations. Due to its detrimental effects on ecosystems, managers have invested substantial effort towards removing the shrub. Albeit many studies have explored the negative effects that Amur honeysuckle has on avian species, there is a lack of research that identifies how removing the shrub impacts birds, especially in rural areas. In order to help optimize management strategies in this regard and better understand how removing this shrub influences birds, I investigated how Amur honeysuckle removal in rural riparian forests affects the composition of avian assemblages.

To accomplish this, I identified plots along the Little Miami River in Greene County, Ohio that are either invaded by or removed of Amur honeysuckle. During the 2019 peak breeding season, I performed avian point counts in order to survey avian assemblages and collected vegetation data in order to measure Amur honeysuckle prevalence and differences in habitat structure and composition among plots. I used a non-metric multidimensional scaling ordination and analysis of similarity to explore differences in avian community structure between plot types and determine whether a community difference existed. I used N-mixture and generalized linear models to explore the impact of removal on avian abundances and species richness and diversity respectively.

I found that avian community composition was different between plots removed of Amur honeysuckle and plots invaded by Amur honeysuckle. The variation in avian community structure was explained, in part, by Amur honeysuckle removal. Avian species were overall more abundant in removed plots. Greater abundances of woodpeckers and species that prefer open woodlands were found in plots removed of Amur honeysuckle vs. plots invaded by Amur honeysuckle. While Amur honeysuckle removal had a positive effect on the Acadian flycatcher (*Empidonax virescens*), other species, i.e., the American robin (*Turdus migratorius*), blue-gray gnatcatcher (*Polioptila caerulea*), Carolina wren (*Thryothorus ludovicianus*), indigo bunting (*Passerina cyanea*), northern cardinal (*Cardinalis cardinalis*), northern parula (*Setophaga americana*), combined tufted titmouse (*Baeolophus bicolor*) and Carolina chickadee (*Poecile carolinensis*), and red-eyed vireo (*Vireo olivaceus*), were unaffected. Avian species diversity and richness appeared to be greater in areas removed vs. invaded by Amur honeysuckle. These findings provide insight to land managers in southwest Ohio regarding how the removal of Amur honeysuckle in rural riparian forests impacts avian community composition.

Dedication

In honor and memory of Dr. John Nagle, a close, life-long mentor of mine, I dedicate this thesis. John, thank you for your thoughtfulness, perspective, and ever cheerful and heartfelt presence, for the always-invigorating conversations over coffee, for taking me under your wing, teaching me so much, and ever inspiring my intrigue.

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Fields of Study

Major Field: Environment and Natural Resources

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Chapter 1: Introduction

Non-native species that become invasive pose a serious threat to native ecosystems (Ruesink et al. 1995, Wilcove et al 1998). Exotic, invasive plants are known to decrease native biodiversity as well as modify habitat and ecosystem processes (Hejda et al. 2009). Although generally framed in a negative manner, alien plant invaders can have some positive effects. For example, some invasive plants provide shelter and/or nutritious food for wildlife in disturbed places where native plants have difficulty establishing (Schlaepfer et al. 2011). In order to fully understand the nuances of the impacts of non-native plant invasion on native biodiversity, invasive plants must be investigated thoroughly (Gurevitch and Padilla 2004, Sagoff 2005).

Amur honeysuckle (*Lonicera maackii*, hereafter referred to as honeysuckle) is a shrub native to Asia that has become highly invasive in the eastern United States since its introduction (Luken and Thieret 1996). The shrub is known to suppress native plant growth and form extensive understory thickets (McNeish and McEwan 2016). Honeysuckle was introduced to southwest Ohio in the late 1950s and is now rampant throughout the state, found in at least 56 of Ohio's 88 counties (Hutchinson and Vankat 1998, Kartesz 2015). Forest habitat has been degraded significantly because of honeysuckle invasion (Bartuszevige et al. 2006). In terms of avian species, habitat dominated by honeysuckle has differential but mostly negative impacts. In the fall and winter, the shrub provides plentiful berries that, although offering poor nutritional value, may be an important food source to birds (Gleditsch and Carlo 2011). However, during the avian breeding season the shrub represents an ephemeral ecological trap, where nests built in honeysuckle are less successful than those built in native woody plants (Rodewald 2012a). Honeysuckle-dominated habitat also impacts avian species composition by, for example, attracting generalist species (McCusker et al. 2010).

Due to its detrimental impacts on ecosystems, land-managers throughout honeysuckle's invasive range are making substantial efforts towards its removal. After honeysuckle removal, plant communities have shown promising responses, e.g., regeneration of the herbaceous layer (Runkle et al. 2007). These changes in plant communities could have cascading effects on bird assemblages.

Although many studies have explored the impact that honeysuckle has on birds, more research is needed in order to determine how birds might be impacted by its removal (McCusker et al. 2010). The goal of this study was to explore how the removal of honeysuckle affects avian community composition specifically in rural riparian forests. To date, no studies have explored how honeysuckle removal impacts avian species in a rural setting. Because of this and the fact that avian community structure changes along a rural to urban gradient (i.e., there is increased prevalence of specialists in rural settings; Croci et al. 2008, Evans et al. 2018), honeysuckle removal in a rural setting could have a more drastic restorative effect. The impact of honeysuckle removal specifically in riparian forests warrants research as removing honeysuckle along waterways has been shown to alter the function of riparian forest ecosystems (McNeish et al. 2012) and rural riparian forests provide vital refuges to wildlife in otherwise homogeneous agricultural landscapes (Smith et al. 2008). Understanding the implications of invasive species removal on avian species is a crucial step towards advancing management strategies. A better understanding of how honeysuckle removal alters avian assemblage composition in rural riparian forests will help optimize management strategies and mitigate impacts to birds.

Chapter 2: Literature Review

Invasive Amur Honeysuckle

Amur honeysuckle, a shrub species that originates from Japan, Korea, Russia, and China, was introduced to North America in the late 1880s (Luken and Thieret 1996, McNeish and McEwan 2016). For many years, it was thought that honeysuckle rejuvenated the land and benefited birds - even the USDA Soil Conservation Service promoted its use in yard plantings until the mid-1980s (Dillon 1981, Luken and Thieret 1996). Over time, honeysuckle has become highly invasive in the midwestern and northeastern regions of the USA (present in over 27 states), especially in disturbed areas where, within only ten years, it can form dense, understory monocultures (Luken and Thieret 1996, Hutchinson and Vankat 1997, McNeish and McEwan 2016, Kartesz 2015). Ironically, the shrub is now considered threatened in its native range (Lieurance and Cipollini 2012).

Honeysuckle is a successful invader in the USA because it grows rapidly (up to 15 feet tall and wide in 10 to 15 years), is morphologically plastic (i.e., can tolerate extreme weather and a broad range of habitats), and is not significantly prone to any diseases, pests, or predators (except deer during early spring and a leaf blight fungus; Luken et al. 1995, Luken et al. 1997, Lieurance and Cipollini 2012, Boyce et al. 2014, Wright et al. 2019). Early spring greenup and late-fall leaf abscission as compared to its native plant counterparts (McEwan et al. 2009) as well as potentially allelopathic tendencies (Dorning and Cipollini 2006, Cipollini et al. 2008, McEwan et al. 2010, Cipollini and Flint 2013) also facilitate invasion. Simply put, the shrub shades out and releases chemicals (via its roots and the decomposition of fallen fruits and leaves) that suppress surrounding native plant-competitors. Thus, in forests where honeysuckle is present, significant adverse impacts on native plant fitness, fecundity, and growth have been shown (Gould and Gorchov 2000, Miller and Gorchov 2004). Research also demonstrates that honeysuckle could be, itself, a facilitator of other non-native invasive plants (Culley 2016).

Relationships between honeysuckle and native fauna help enable the shrub's spread (McNeish and McEwan 2016). Honeysuckle's white to light orange tubular flowers bloom in the spring and, if pollinated, begin to transform into bright red berries in the late-summer (Bartuszevige and Gorchov 2006). Honeysuckle can be a superabundant food source, with an individual shrub producing up to 1.2 million berries in a year (Ingold and Craycraft 1983). Although a variety of animals eat these berries and disperse viable honeysuckle seed (e.g., white-footed mice and deer), birds are its predominant dispersers (Castellano and Gorchov 2013, McNeish and McEwan 2016). For overwintering and migrating avian species, non-native shrubs in general have been shown to be a potentially important food resource (Reichard et al. 2001). Although many frugivorous avian species eat honeysuckle berries, only a portion of them disperse viable honeysuckle seed (Ingold and Craycraft 1983, Bartuszevige and Gorchov 2006), with the American robin (*Turdus migratorius*) likely being the primary disperser of the shrub. Because the American robin benefits from the shrub as a fall/winter food source and in turn scatters shrub seeds farther than possible for non-avian frugivorous wildlife, some propose that a mutualistic relationship between honeysuckle and the American robin has formed (Bartuszevige and Gorchov 2006, McCusker et al. 2010, Gleditsch and Carlo 2011). Indeed, the spread of honeysuckle might even be partially responsible for a shift in the winter range of the American robin (i.e., the American robin has followed the spread of this fall/winter food source northward; McCusker et al. 2010).

Honeysuckle has no doubt changed the landscapes where its invasion has occurred. Studies show that disturbed areas such as unmowed roadsides and fence lines (Luken 1988), waterway banks (Medley 1997), secondary forests (Hutchinson and Vankat 1997), and areas that have been impacted by emerald ash borer (Klooster et al. 2018) are more susceptible to honeysuckle invasion (Flory and Clay 2005, Flory and Clay 2009). Old growth forests and forests with taller trees seem to be more resistant to invasion (Hutchinson and Vankat 1997). At the landscape scale, forest cover and connectivity between forests (Hutchison and Vankat 1998), highway and urban river corridors (Pennington et al. 2010), patches of habitat that are evenly dispersed (Hutchison and Vankat 1998), forest edge habitat (Borgmann 2002, Bartuszevige et al. 2006), and proximity to development, urban areas or invaded sites are associated with honeysuckle invasion and its facilitation (Hutchison and Vankat 1998, Borgmann and Rodewald 2005, Bartuszevige and Gorchov 2006, Trammell and Carreiro 2011, White et al. 2014). Honeysuckle invasion seems to be stifled by matrix areas that are filled with vast expanses of agricultural land; thus, forests isolated by agriculture are less susceptible to invasion (Hutchison and Vankat 1998). Many of these patterns are likely driven by avian movements on the landscape and thus seed dispersal (Hutchison and Vankat 1998).

The Impact of Amur Honeysuckle on Avian Species

Avian species are, in general, negatively impacted by honeysuckle. Resident and short distance migrants tend to be more prevalent in areas dominated by honeysuckle whereas long distance migrants show the opposite trend (Rodewald 2005). Understory species like the wood thrush (*Hylocichla mustelina*) and gray catbird (*Dumetella carolinensis*), seem to prefer honeysuckle-invaded areas while canopy species, like the eastern wood-pewee (*Contopus virens*), red-eyed vireo (*Vireo olivaceus*), and Paridae species such as the tufted titmouse (*Baeolophus bicolor*) and Carolina chickadee (*Poecile carolinensis*), do not (McCusker et al. 2010, Lynch 2016). Most species that are positively associated with honeysuckle-abundant areas are generalists, like the northern cardinal (*Cardinalis cardinalis*) and American robin (especially in the fall/winter), i.e., species that are not usually of conservation concern, while those that are negatively associated tend to be specialists, e.g., the Acadian flycatcher (*Empidonax virescens*) (McCusker et al. 2010, Rodewald 2012a, Rodewald 2012b, Lynch 2016). All of these trends are likely due to the habitat structure and composition changes that accompany honeysuckle invasion, especially those that impact the availability of preferred food, nest substrates, and nesting sites (Rodewald 2005). For example, the reduced number of Acadian flycatchers and eastern-wood pewees, both aerial foragers, in honeysuckle-dominated habitat may be a response to the dense understory that honeysuckle creates, a factor that may prohibit efficient aerial foraging (Rodewald 2005, McCusker et al. 2010). Conversely, the positive association of shrub-nesters, like the northern cardinal, American robin, and gray catbird, with habitat invaded by honeysuckle might be due to the increased amount of potential nest sites that these habitats provide (McCusker et al. 2010). Although some of these species, upon first look, appear to benefit from the shrub's presence, i.e., by using the shrub as a source of food and/or nesting site during breeding season, they might actually be caught in a "trap" that causes more harm than good as detailed below (Rodewald 2012a).

Some avian species do not recognize honeysuckle berries as food perhaps due to lack of coevolution or the fact that its berries offer low-quality nutrition (with only 3-5% fat content as compared to the 30-50% fat content of the average native plant fruit) (Ingold and Craycraft 1983, Smith et al. 2013). Nevertheless, other frugivorous avian species, as previously mentioned, use the berries as a fall/winter food source, namely the American robin, cedar waxwing (*Bombycilla cedrorum*), northern mockingbird (*Mimus polyglottos*), American goldfinch (*Spinus tristis*), gray catbird, northern cardinal, hermit thrush (*Catharus guttatus*), and European starling (*Sturnus vulgaris*) among others (Bartuszevige and Gorchov 2006, Gleditsch and Carlo 2011). During winter months, frugivorous birds tend to be substantially more prevalent in areas dominated by honeysuckle, likely because the vast majority of fruits available during the winter are honeysuckle berries (Reichard et al. 2001, McCusker et al. 2010, Gleditsch and Carlo 2011). Some birds even seem to have a preference for honeysuckle fruit over higher quality fruits from native species potentially because birds tend to choose fruit based on conspicuousness and quantity (Sallabanks 1993, Vila and D'Antonio 1998, Drummond 2005, Lynch 2016). Gleditsch and Carlo 2014 found that healthy fledgling physiology (higher mass:tarsus ratios) of the gray catbird in honeysuckle-invaded areas may be due to honeysuckle fruit abundance. Some studies indicate that honeysuckle berries may create false indicators of avian fitness via enhancing the plumage coloration of, e.g., northern cardinals, if eaten - an ecological trap (Witmer 1996, Jones et al. 2010). However, Hudon and Mulvihill (2017) suggest that these plumage changes are due specifically to the fruits of different *Lonicera* species, i.e., *Lonicera morrowii* and *Lonicera tatarica*, as the carotenoid known to change coloration in this way, Rhodoxanthin, is present in their berries, but not in *Lonicera maackii* fruits. Berries from these other non-native *Lonicera* species present in the Eastern USA have been shown to cause plumage changes in the yellow-shafted flicker (*Colaptes auratus auratus* - a subspecies group), cedar waxwing, and Baltimore oriole (*Icterus galbula*) in addition to other species (Brush 1990, Hudon et al. 2013, Hudon et al. 2017, Hudon and Mulvihill 2017).

Honeysuckle is likely an ephemeral ecological trap to birds during the breeding season. Early green-up may make honeysuckle appear to be an attractive nesting spot, with certain species, particularly the northern cardinal, preferentially choosing honeysuckle as nesting habitat over native plant species in urban areas (Leston and Rodewald 2006, Rodewald et al. 2010). However, nests built in honeysuckle by the northern cardinal and American robin were found to be predated on more frequently with northern cardinal nests fledging 20% fewer offspring in honeysuckle than in native woody species in urban areas (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Rodewald et al. 2010). This trend disappears for the northern cardinal later in the breeding season, but not for the American robin, likely because the northern cardinal breeding season begins earlier than most birds, including the American robin - predators likely focus their efforts on northern cardinal nests earlier in the season since there are less other nests available (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Rodewald et al. 2010). Interestingly, the increased predation of northern cardinal and American robin nests occurred in urban but not rural areas (Borgmann and Rodewald 2004). However, artificial nest experiments demonstrate that invaded rural areas are still at risk of reduced nest success (Borgmann and Rodewald 2004). Furthermore, Acadian flycatcher nests built in honeysuckle are associated with increased brood parasitism by the brown-headed cowbird (*Molothrus ater*) (Rodewald 2009). Thus, nests built in honeysuckle tend to have lower nest productivity when compared to those built in native shrubs. Increased nest predation rates may be explained by higher shrub volume surrounding nests in honeysuckle-invaded areas as well as lower nest height, which, for mammalian nest predators, increases the accessibility of prey and thus search efficiency (Schmidt and Whelan 1999, Borgmann and Rodewald 2004). Other shrub-nesters, such as the gray catbird and wood thrush are also known to nest in honeysuckle (McCusker et al. 2010).

Because non-native plant species generally support significantly lower amounts of arthropods than native species (Tallamy 2009), honeysuckle might have bottom up effects on the food web that impact avian insectivores. Studies show that the shrub has differential impacts on available food resources for insectivorous avian species. Increased abundances but not diversity of spider taxa were found in honeysuckle invaded vs. non-invaded areas - likely due to the branching structure of the shrub (Loomis et al. 2014a).

This might suggest increased food resource levels for avian foliage gleaners, with vertical cover in invaded plots more than double the amount in non-invaded plots. Further support for this claim is demonstrated by Loomis et al. (2014b), where honeysuckle-invaded plots had higher abundances of Hymenoptera, Hexapoda, Psocoptera, and Diptera, species diversity of Coleoptera, Psocoptera, and Hexapoda, and species richness of Psocoptera, Diptera, Hexapoda, Hymenoptera, and Coleoptera; evenness, however, was similar between honeysuckle-invaded and not-invaded plots. These results might be explained by honeysuckle structural attributes, favorable microclimates, and/or higher amounts of available resources, e.g., food and shelter (Loomis et al. 2014b). Because honeysuckle releases allelochemicals, changes the soil microbial community and decomposition rate of leaf litter (Blair and Stowasser 2009, Arthur et al. 2012, Trammell et al. 2012), and shades the soil throughout the growing season (Watling et al. 2011), it might, in turn, impact ground-dwelling arthropods, an important resource for ground-foraging birds. In this regard, studies, at present, only show that honeysuckle might negatively impact ground-dwelling spiders (Buddle et al. 2004) and positively affect the biomass of exotic earthworms, but have no impact on exotic earthworm density (Lloyd et al. 2019).

Management of Amur Honeysuckle and Its Implications for Avian Species

Land managers have made considerable efforts to remove honeysuckle because of its deleterious effects on ecosystems. Management of honeysuckle has included painting herbicide onto cut stumps, cutting then later spraying stem regrowth with herbicide, foliar or basal bark application, and injecting herbicide into cut stumps (McNeish and McEwan 2016). Research generally points to application of herbicide to honeysuckle stumps immediately post-cutting as the most effective management strategy (McNeish and McEwan 2016). Multiple studies have demonstrated the importance of continued, usually minor, honeysuckle management after the first removal event (McNeish and McEwan 2016, Hopfensperger et al. 2019). At least five years after honeysuckle removal, studies have found increases in tree seedling density, species richness, herbaceous cover, and plant cover (Runkle et al. 2007, Hopfensperger et al. 2019). Hartman and McCarthy (2004) found that, three years post-removal of honeysuckle, seedling survivorship of native species was greater in removed than invaded areas, though this varied among genera.

Honeysuckle removal could play an important role in increasing the abundances of certain avian species. For example, studies have found that removing or thinning understory vegetation increases the abundance of eastern wood-pewees (Wilson et al. 1995, Rodewald and Smith 1998). Gleditsch and Carlo (2011), however, caution that honeysuckle removal could have negative impacts on frugivorous bird species in the fall/winter, stripping them of an abundant food source. Others expect that removing honeysuckle, causing a temporary but almost complete elimination of an important forest layer (the understory), might discourage shrub-utilizing species from using restored areas until native shrubs have regenerated several years later (McCusker et al. 2010). McCusker et al. 2010 recommends that honeysuckle removal be supplemented by replacement-plantings of native shrubs that provide needed resources (i.e., nesting sites and food) in order to mitigate short-term negative impacts on birds. An alternative management method is proposed by a study that investigated the impact on avian species of different strategies for removing another invasive shrub species, Russion Olive (*Elaeagnus angustifolia)*: removing the invasive shrub in a stepwise, interspersed manner such that the structural complexity required by birds is maintained while matrix areas of removal regenerate with native species before the remainder of invading shrubs are removed (Valente et al. 2019). Although there have been multiple calls from researchers, bird enthusiasts, and land managers alike to investigate the impact of different honeysuckle removal techniques on birds (McCusker et al. 2010, Lynch 2016, McNeish and McEwan 2016), the topic remains understudied. Presently, only honeysuckle removal impact on bird-plant networks in urban riparian forests has been explored, certifying that ecological network structure was not restored post-honeysuckle removal, possibly due to time-lags in recovery (Rodewald et al. 2015).

Honeysuckle removal impacts on avian insectivore prey, on the other hand, has received more attention. Christopher and Cameron (2012) found that immediately post-honeysuckle removal, litter-dwelling arthropod diversity and abundance resembled that of honeysuckle-absent areas while the abundance of ticks/mites and spiders decreased and increased respectively. However, Masters et al. (2017) found that these restorative impacts might be temporary: one year post-removal, there was an increase in overall (i.e., aerial and ground-dwelling) arthropod diversity in removed sites, but no difference between treatments in terms of overall arthropod abundance; three years post-removal, removed plots consisted of lower abundance and richness of ground-dwelling arthropods that was explained, in part, by other shrubs in the plots. Pipal (2014) found a lower biomass and density of exotic earthworms in honeysuckle removed vs. invaded plots four to five years post-removal. However, Mahon and Crist (2019) experienced slightly differing results where the removal of honeysuckle (in 2010 with follow-up removal in 2015) resulted in a reduction in earthworm biomass only when deer were excluded, and had no impact on the density of earthworms (sampled 2013-2017). In the same study system, the abundance and richness of ants decreased in plots where honeysuckle removal occurred, likely due to changes in vegetation structure and the biomass of litter (Mahon et al. 2019). In sum, the impact of honeysuckle removal on arthropod communities is currently unclear due to conflicting results between studies - further research is required before solid conclusions can be made.

Objectives and Hypothesis

In order to explore the effects of honeysuckle removal on the composition of avian communities in rural riparian forest, I surveyed birds and vegetation in plots both invaded by and removed of honeysuckle along a river in rural southwest Ohio. The objectives of my study were to characterize any differences or similarities that exist in the following between areas of rural riparian forest that were invaded by and removed of honeysuckle: 1) avian community structure, 2) the abundance of species guilds, the ten most commonly observed avian species, and all species combined, and 3) avian species richness and diversity. Because studies have shown that honeysuckle-dominated areas have a different composition of avian communities than areas not invaded by honeysuckle, I hypothesized that avian community structure would differ between plots invaded by and removed of honeysuckle. In particular, I expected to find that the abundances of resident-short distance migrants, understory species (namely shrub-nesters), and generalists would be greater in plots dominated by honeysuckle than in areas removed of the shrub as these species guilds are, as previously discussed, associated with honeysuckle-invaded habitat (McCusker et al. 2010, Rodewald 2012a, Rodewald 2012b, Lynch 2016). I also expected that the abundances of long distance migrants, canopy species (namely those that prefer open forest habitat), and specialists would show the opposite trend as these species guilds, as also described above, seem to avoid honeysuckle-invaded plots (McCusker et al. 2010, Rodewald 2012a, Rodewald 2012b, Lynch 2016). Lastly, I hypothesized that avian diversity and species richness would be higher in plots where honeysuckle was removed vs. invading as ecological restoration tends to increase biodiversity (Benayas 2009), and Rodewald (2005) found that avian species richness was (marginally) greater in areas not invaded by honeysuckle than in areas invaded by it.

Chapter 3: Methods

Study Location

In the southwestern corner of Ohio, honeysuckle is the dominant shrub in many forests, causing forest habitat degradation (Hutchinson and Vankat 1997, Bartuszevige et al. 2006). This study took place in southwestern Ohio on public and private land in Greene County along the Little Miami River - a Class I tributary of the Ohio River that is designated as a State and National Scenic River. Multiple parks and nature preserves surround and protect the Little Miami River. The canopy of the riparian forest bordering it consists mainly of black walnut (*Juglans nigra*), Eastern sycamore (*Platanus occidentalis*), osage orange (*Maclura pomifera*), Ohio buckeye (*Aesculus glabra*), honey locust (*Gleditsia triacanthos),* hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), and box elder (*Acer negundo)*. Greene county as a whole is largely composed of agricultural land that surrounds small towns. The total county population is approximately 168,937 (U.S. Census Bureau 2010) with more populated areas typically 2 or more kilometers away from the Little Miami River. This area lies within the Loamy High Lime Till Plains ecoregion, where the climate is humid and soils are loamy and rich in lime (Woods 1998).

Plot Selection

I identified a total of 26 study plots of 130 meters in length along the Little Miami River (Figures 3.1 and 3.2), using the following criteria: 1. topography (slope < 5%), 2. relative vicinity (within 25 km of all other plots), 3. proximity to other plots (non-overlapping), 4. riparian forest habitat of at least 50 meters in width that was either entirely invaded by or removed of honeysuckle, and 5. contiguous land cover and honeysuckle prevalence in the area adjacent to the plot opposite of the river. I determined plot locations remotely, then field verified that selection criteria were met after obtaining permission from the respective land managers and owners to access these locations for this research. I stratified plots by honeysuckle status: invaded vs. removed. I used plots that are still mostly invaded by honeysuckle (8 total) as controls, and compared them with plots where effective removal occurred (18 total; Figure 3.1).

The majority of study plots fell within the southern portion of the Glen Helen Nature Preserve (14 total) - a nature reserve adjacent to Antioch College that, in addition to adjacent natural areas, the Ohio Department of Natural Resources deems “exceptional” in terms of ecological significance. Other plots fell within the Narrows Reserve (7 total) and private land (2 total) as well as in natural areas directly adjacent to the Glen Helen Nature Preserve: John Bryan State Park (2 total) and the Little Miami State Forest Preserve (1 total). Among the honeysuckle-removed plots, honeysuckle management treatments and time since removal vary: managers cut honeysuckle and painted stumps with 50% glyphosate in 12 northern plots (within the Glen Helen Nature Preserve) once between 2014 and 2016 (10 in 2014 and 2 in 2015-2016), and managers sprayed all honeysuckle present with 1-1.5% glyphosate solution (foliar application) in the 7 southernmost plots (the Narrows Reserve) almost every year from 2010-2016 (Figure 3.1). The amount of honeysuckle in plots occasionally differed substantially from the amount of honeysuckle found in the respective plot-bordering areas, e.g., honeysuckle-invaded plots bordered directly by honeysuckle-removed areas and vice versa.

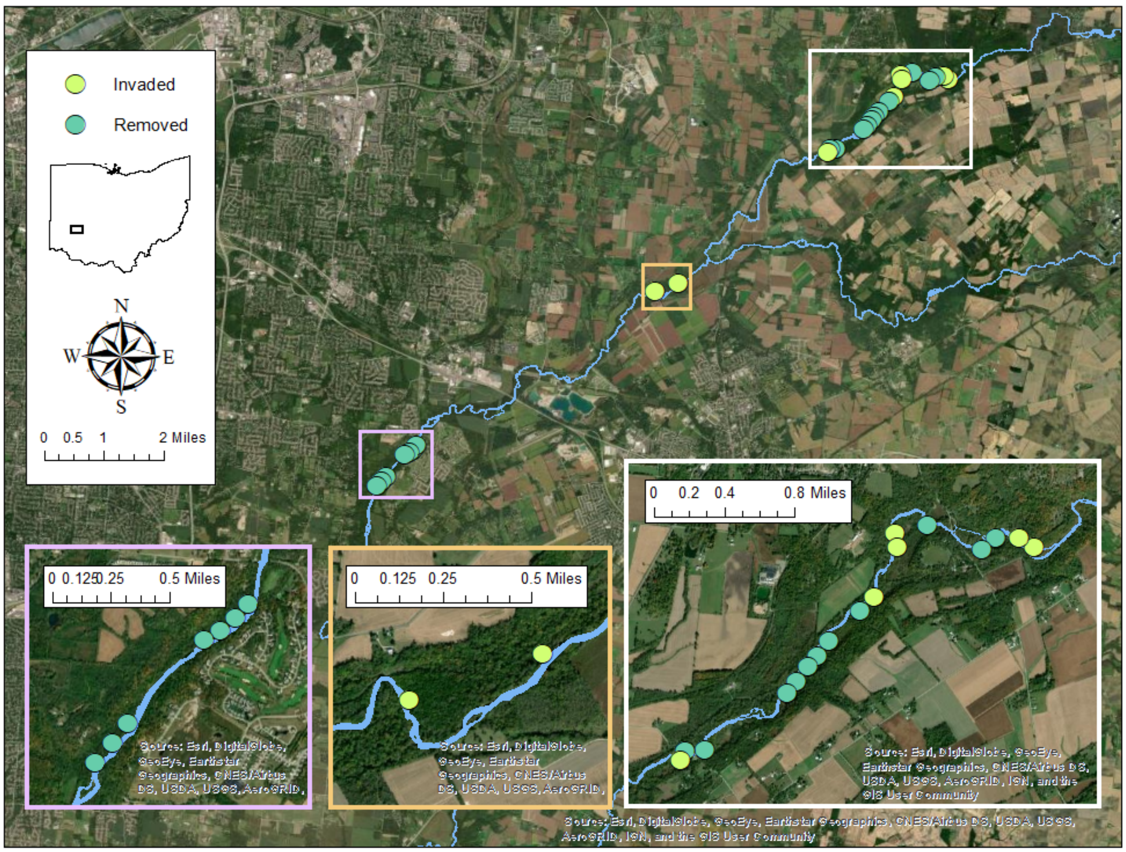

Figure 3.1. Plot locations along the Little Miami River in Greene County, Ohio.

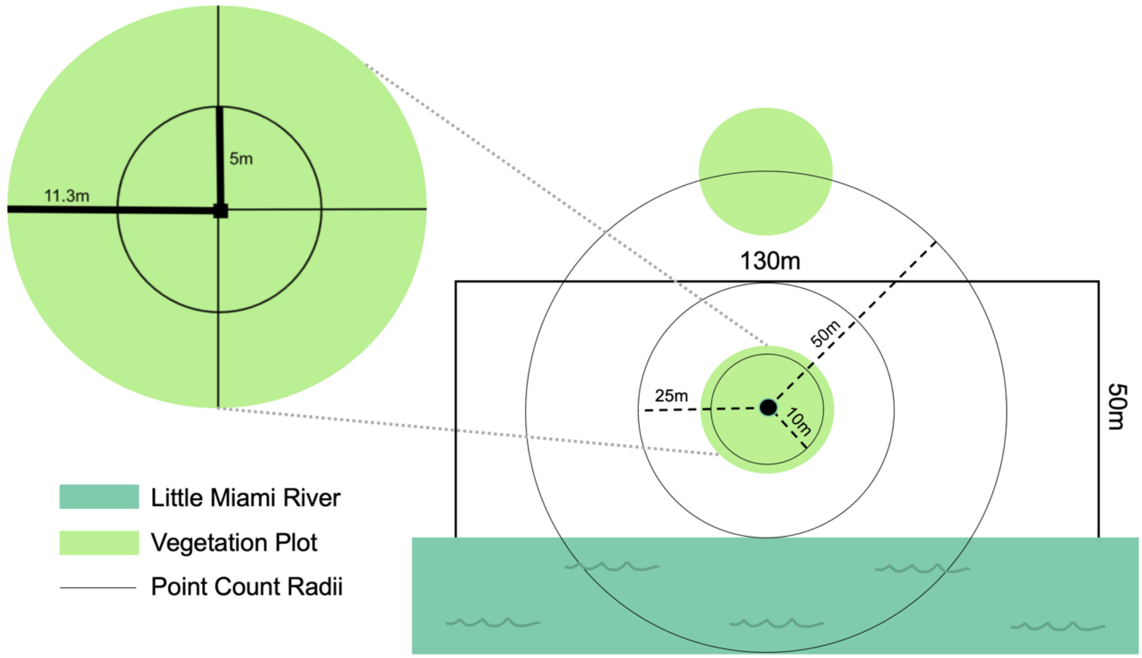

Figure 3.2. Plot structure (right) with the black dot marking the plot midpoint and location where point counts occurred. Smaller green circles designate vegetation survey locations relative to the plot. Thin, black-outlined circles indicate point count radii (10m, 25m, and 50m). Vegetation survey plot structure (left) with inner, black-outlined circle designating the 5m circular plot within the entire filled green circle which designates the 11.3m radius plot.

Vegetation Surveys

During June and July 2019 I surveyed the vegetation at all plot midpoints in order to attain plot measures of honeysuckle and habitat composition and structure (Figure 3.2). I also surveyed the vegetation at a location 50m away from the plot midpoint in the opposite direction of the river (Figure 3.2). I followed protocol adapted from Martin et al. (1997) for all vegetation surveys. This method establishes 5 and 11.3m radius (400m^2)

circular plots divided with ropes into quadrants using cardinal directions (Figure 3.2). I took GPS coordinates at the center of each plot using handheld GPS units. Within vegetation plots I measured the following:

Overstory Composition and Structure

Within the entire 11.3m radius, I measured the diameter at breast height (DBH) of all woody plants greater than 8cm DBH and greater than 3m in height - live and dead - identifying all live individuals to species. I used a hypsometer to measure the canopy base height (CBH) and height of the two live trees (again > 8cm DBH and > 3m in height and within the 11.3m radius) in each quadrat that were closest to the vegetation plot midpoint. I used DBH measures to calculate the total basal area of each vegetation plot and CBH and height measures to derive the average canopy height and crown length of every vegetation plot. I also counted all DBH-measured snags to obtain a frequency of snags for each vegetation plot. In order to measure canopy cover, I used a GRS densitometer and the point intercept method (Caratti 2006a), with the 11.3m quadrat boundaries serving as transects and survey points every two meters, to determine whether each point "hit" or "missed" the canopy. I recorded the overall percent of "hits" as the canopy cover for the vegetation plot.

Understory Composition and Structure

I used a vegetation sampling pole and the point intercept method (Caratti 2006a; again, 11.3m quadrat boundaries serving as transects, survey points occurring every two meters) to identify to species and count all intercepting stems of woody plants less than 8 cm DBH and between 0.5m and 3m in height. I used these measures to determine the frequency of native woody stems, invasive woody stems, honeysuckle stems, and woody stems overall in the understory of each vegetation plot. To calculate the percent cover of native woody plants, invasive woody plants, and honeysuckle as well as overall woody cover in the vegetation plot understory, I used the line intercept method (Caratti 2006b) with 11.3m quadrat boundaries serving as transects to document and identify to species all woody plants less than 8cm DBH and between 0.5m and 3m in height.

Ground Layer Composition

At every vegetation plot within each quadrat bounded by the 5m radius, I visually estimated percent ground cover broken into 7 cover classes using the Domin scale (Sutherland et al. 2006). The cover categories I used are as follows: bare ground, leaf litter, woody seedling less than 0.5m tall, forb, graminoid, fern, and log/stump.

Avian Surveys

To measure avian habitat use, I visited each plot three times between sunrise and 1030h during the peak breeding season, May through early July, of 2019 with at least two weeks separating visits. I used the point count method (Ralph et al. 1993) to survey avian species. I chose the point count method over other avian survey techniques because it has been adopted as the standard avian monitoring method and, for most avian surveys, is the best option as it is data-rich and efficient, especially in forested habitats (Ralph et al. 1993). For each point count, I stood at the plot midpoint and recorded every bird that I heard over a 10-min period. I took note of birds observed visually but not heard and/or flying over, but did not record these as counts as honeysuckle prevalence in invaded plots but not removed plots obstructed visual observations and individuals flying over were not technically in the plot. I recorded species observed within zero to 10m, 10 to 25m, 25 to 50m and greater than 50m radii of the plot midpoint (Figure 3.2). To optimize the chance that recorded birds were truly within point count radii classes, I used a laser range finder to calibrate distance estimations before conducting each point count. Also prior to performing each point count, I recorded noise level (on a scale from one to three) and weather data including percent cloud cover (visually estimated), temperature, and wind speed (the latter two measured with a Kestrel handheld pocket weather meter) as well as presence of any flooding or temporary pools of water within the plot. In order to increase detection probabilities, I did not perform point counts if there was rain, wind gusts greater than 20 mph, low visibility due to fog, or significant flooding within the plot. To avoid observer bias, I alone performed all point counts. I recorded any birdsong that I heard and did not recognize with a digital recorder for later identification.

Analysis

Vegetation

I used unpaired t-tests and Man-Whitney U tests to examine whether each within-plot habitat measure differed between honeysuckle-removed vs. invaded plots (alpha = 0.05). I performed Mann-Whitney tests on the diversity of woody species in the understory, percent ground cover of bare ground and leaf litter combined, percent groundcover of woody seedlings, and all but one - overall percent cover of woody plants in the understory - of the measures of woody cover and stems in the understory as these habitat parameters did not meet the assumptions for unpaired t-tests (even after variable transformation attempts). I used Shapiro-Wilks tests of normality and F-tests of homogeneity to determine whether assumptions were met. All other parameters met the assumptions for unpaired t-tests - some only after I performed square-root transformations, i.e., basal area of canopy trees and percent groundcover of logs/stumps and forbs, and overall percent cover of woody plants in the understory and frequency of snags only after a double square-root transformation.

In order to account for the community structure of canopy trees among plots, I created a variable representing the community composition of canopy trees by ordinating the structure of canopy tree communities among plots using non-metric multidimensional scaling (NMDS) (Program R package: vegan, Oksanen 2011, v 3.5.2, R Core Development Team 2018, Oksanen et al. 2019). NMDS is a nonparametric, multivariate procedure that takes multidimensional data and, retaining as much information as possible, reduces the data down to two or three dimensions in order that trends can be more easily interpreted, i.e., it maximizes the rank correlation between distances in the reduced ordination space and distances in the original multidimensional matrix (Oksanen et al. 2011). This method allows for the use of the Bray-Curtis dissimilarity calculation, which is ideal when it comes to species abundances as, for example, it is robust to the many zeros involved with count data. I used a Bray-Curtis dissimilarity matrix and excluded species occurring in less than 5% of samples (Kennedy et al. 2010). I used the axis ordination score of each study plot from the axis that explained the greatest percent of variation as the data values for the canopy composition of each plot.

Avian Community Composition

To better ensure independence between plots in terms of observed avian communities, I truncated the point count data to only include birds observed within the 50m radii around the plot midpoint for all avian analysis. I did not truncate by the 25m radii, even though this would better ensure that the observed individuals fell within plots, because doing so would make the sample size too small for the abundance analysis. In all avian analysis, I included only species that are known to breed in the study area (eBird 2019, Table A.1.).

To visually explore the avian community structure in plots invaded by and removed of honeysuckle, I used an NMDS ordination with the Bray-Curtis distance index as the distance measure. I only included avian species that occurred in more than 5% of samples (Kennedy et al. 2010). I combined certain species together to account for potential misidentifications: Carolina chickadee with tufted titmouse, European starling with brown-headed cowbird, and all woodpecker species. To explore how different habitat characteristics might factor into each NMDS axis gradient, I correlated habitat variables onto them.

I paired this NMDS ordination with an analysis of similarity (ANOSIM) for significance testing (Program R package: vegan, Oksanen et al. 2011, v 3.5.2, R Core Development Team 2018, Oksanen et al. 2019). ANOSIM is a nonparametric, permutation test of among-group differences, i.e., of whether two or more groups of entities - in this case, avian assemblage structure grouped by honeysuckle status - differ from each other (Chapman and Underwood 1999). I used the *P*-value (alpha = 0.05) to examine whether avian community composition was different between honeysuckle-invaded vs. removed plots.

Avian Species Abundance, Diversity, and Richness

To explore the impact of honeysuckle removal on avian species richness and Shannon diversity, I used generalized linear models (GLMs) (Program R, v 3.5.2, R Core Development Team 2018). I used N-mixture models (pcount function in Program R package: unmarked, v 3.5.2, Fiske and Chandler 2011, Chandler and Royle 2013, Denes et al. 2015, R Core Development Team 2018) to explore the effects of honeysuckle removal on the abundances of all songbirds combined, the ten most commonly observed avian species, and species within different guilds: shrub-nesters, species that prefer open woodland habitat, and resident-to-medium and medium-to-long distance migrants (Billerman et al. 2020). N-mixture models are hierarchical, simultaneously estimating the probability of detection and abundance of avian species over multiple visits to survey locations (Chandler and Royle 2013). This provides a way to account for the imperfect detection of avian species, resulting in more accurate abundance estimates. I assessed the following observation-specific detection covariates: temperature, percent cloud cover, wind speed, time of day, number of days since first point count, and noise level. I set detection functions for all abundance models as the highest-ranking variable combination derived from a model set consisting of all possible additive combinations of detection covariates.

When determining the most commonly observed species, I combined counts of European starling and brown-headed cowbird as well as all woodpecker species except for the pileated woodpecker (*Dryocopus pileatus*) and northern flicker (*Colaptes auratus*) to account for potential misidentifications. Although both the group of woodpecker species and combination of European starling and brown-headed cowbird fell within the top ten most frequently observed species, I did not include them in the top ten species abundance analysis because the latter included species with different niches and I decided to combine the former with the pileated woodpecker and northern flicker for abundance analysis regarding the entire woodpecker guild since I had already grouped most of the woodpecker species. Because the woodpecker guild contained comparatively numerous species, it did not make sense to consider it as an individual species. Prior to the analyses of abundance and species diversity and richness, I standardized all independent variables used in the models and screened for covariance between variables (with a 0.7 threshold) as well as transformed them when appropriate in order to reduce data heterogeneity of variance and non-normality.

I utilized a set of candidate models that I developed *a priori* for all abundance functions in the abundance model analyses and the avian species diversity and richness model analyses. The candidate model set (Table 3.1) consisted of the following habitat variables: the within-plot NMDS-derived composition of tree species in the canopy, average of standardized percent groundcover of logs/stumps and frequency of snags (calculated after performing square-root and double square-root transformations on the variables respectively), canopy cover, basal area of canopy trees (square-root transformed), crown length of canopy trees, honeysuckle percent cover, and honeysuckle status as well as the average of standardized plot-bordering honeysuckle cover and frequency of honeysuckle stems (calculated after performing double square-root transformations on both). Because I was mainly interested in the effect of honeysuckle removal, I chose to include plot honeysuckle status in most models - with only two strictly canopy models - in order to obtain the best possible estimates of the effect size and predictions of the impact of honeysuckle removal. Since I would use the model set widely, I varied habitat parameter combinations with plot honeysuckle status in an attempt to capture a broad and meaningful range of habitat preferences. Within-plot amount of woody cover, invasive woody cover, honeysuckle cover, woody stems, invasive woody stems, and honeysuckle stems in the understory as well as percent groundcover of forbs, and percent ground cover of bare ground and leaf litter combined were all highly correlated and redundant with plot honeysuckle status. Of these variables, I chose only to include honeysuckle percent cover in the model set in order to evaluate a competing hypothesis of whether honeysuckle status or measured level of honeysuckle invasion vs. removal better predict avian abundances, richness and diversity as some plots that were categorized as invaded had a slightly higher level of invasion than others. I chose honeysuckle cover over frequency of honeysuckle stems to evaluate this because, based on my observations, it better represented the honeysuckle invasion level of invaded plots. I included the plot-bordering honeysuckle variable because bird territories likely extended beyond the width of the plots and thus accounting for this could have helped yield better predictions of avian response to honeysuckle status within plots. To assess the possibility that the predictors in the model set did not explain the data, even if there was a difference, I included null models. I excluded variables, such as measures of native woody plants in the understory and groundcover as they were sparse, with maximum values that did not logically appear to be biologically significant enough to make a difference on avian abundance. I also excluded height and diversity of canopy trees as they provided information that was redundant with other canopy variables. It is possible that, because I included honeysuckle status in most models within the candidate model set, a type I error occurred as the prevalence of the variable within the model set made the possibility of finding an effect by chance more likely.

I analyzed all abundance, richness, and diversity models with an information theoretic (IT) approach, using Akaike's Information Criterion (AIC) to identify top models (Burnham and Anderson 2002). Because my sample size was small, I considered all GLMs with a modified ΔAIC, i.e., ΔAICc. However, I used AIC instead of AICc for N-mixture model inference as the effective sample size is unclear for these model types (MacKenzie et al. 2006). I examined all models within seven AIC or AICc respectively of the top models (Burnham and Anderson 2002) and averaged models with an AIC (using the unmarked package in Program R predict function) or ΔAICc (Program R package: AICcmodavg, Mazerolle 2019, v 3.5.2, R Core Development Team 2018) respectively of less than two in order to make predictions. To examine the goodness of fit of N-mixture models, I used parametric bootstrapping procedures (1000 simulations) to calculate the sums of squares (SSE), Freeman-Tukey, and Chi-square fit statistics for the global model and all models within a ΔAIC of two. To determine an appropriate distribution for abundance models, I ran analogous abundance models specifying both Poisson and negative binomial distributions (both commonly used with count data) then assessed the resulting dispersion parameter estimates provided in model outputs. I found no strong evidence of overdispersion for any abundance model - most models tended towards slight underdispersion. Because of this, I specified the Poisson distribution over negative binomial for all abundance models. I did not find evidence of poor model fit for any model, however, fit estimates for some models were very close to one likely due to underdispersion (Table 4.3). For GLMs of species richness and diversity, I used AICc and R^2 to assess the fit of global and top models and choose the most appropriate distribution. Distributions of both species richness and Shannon diversity were normal, so I fitted Gaussian GLMs for both measures. In these models, I accounted for potential species misidentifications by combining counts of European starling and brown-headed cowbird, Carolina chickadee and tufted titmouse, and all woodpecker species except for the pileated woodpecker and northern flicker. Models appeared to fit the data (Table 4.4). For all abundance, diversity, and richness models, I used the *P*-value to assess the importance of honeysuckle and other habitat variables. I considered an alpha less than 0.05, 0.10, and 0.15, as an indicator of a strong, moderate, and weak effect respectively (Buler et al. 2007).

Table 3.1. Candidate model set for avian diversity, richness, and all abundance models.

Name	**Habitat parameters included**
Null model	n/a
Global model	~ Canopy composition + Canopy cover + Basal area + Canopy crown length + Deadwood + Plot-bordering honeysuckle + Honeysuckle status
Honeysuckle status model	~ Honeysuckle status
Honeysuckle cover model	~ Honeysuckle cover
Canopy model	~ Canopy composition + Canopy cover + Basal area + Canopy crown length
Reduced canopy model	~ Basal area + Canopy crown length
Plot-bordering honeysuckle model	~ Plot-bordering honeysuckle + Honeysuckle status
Canopy cover model	~ Canopy cover + Honeysuckle status
Canopy crown length model	~ Canopy crown length + Honeysuckle status
Basal area model	~ Basal area + Honeysuckle status
Canopy composition model	~ Canopy composition + Honeysuckle status
Deadwood model	~ Deadwood + Honeysuckle status

Chapter 4: Results

Vegetation

I observed a total of 14 different canopy tree species across all plots. Box elder (*A. negundo*) was by far the most commonly observed species (n = 150) followed by osage orange (*M. pomifera*, n = 53), black walnut (*J. nigra*, n = 42), American elm (*U. americana*, n = 34), and sycamore (*P. occidentalis*, n = 21) (Figure 4.1). Removed plots were composed of very little understory. Because of this, the woody understory found across both honeysuckle-removed and honeysuckle-invaded plots consisted almost entirely of honeysuckle: approximately 83% and 91% respectively of the overall amount of woody cover and stems in the understory that I observed. Multiflora rose (*Rosa multiflora*) and privet (*Ligustrum* spp.) were the only other invasive woody species found in plot understories, together making up about 3% of the amount of understory woody cover, and less than 1% of the number of understory woody stems. The native woody plants most commonly observed in the understory were Ohio buckeye (*A. glabra*) and box elder (*A. negundo*) saplings, together accounting for approximately 10% and 5% of the amount of woody cover and stems in the understory across plot types respectively. All vegetation measures recorded in plot-bordering areas fell more or less within the range of measures observed in plots (Table 4.1) except for the percent of plot-bordering canopy cover at one plot.

Habitat characteristics differed between plots invaded by vs. removed of honeysuckle (Table 4.1). Percent cover of native woody plants in the understory ($U = 33$,

$P = 0.03$) and percent groundcover of forbs ($t = -4.40$, df = 24, $P < 0.001$) were greater in plots removed of honeysuckle (Table 4.1). In the understory of plots, amount of woody cover ($t = 13.61$, df = 20.59, $P < 0.001$), invasive woody cover ($U = 144$, $P < 0.001$), honeysuckle cover ($U = 144$, $P < 0.001$), woody stems ($U = 131$, $P = 0.001$), stems of invasive shrubs ($U = 144$, $P < 0.001$), and honeysuckle stems ($U = 144$, $P < 0.001$) as well as percent ground cover of bare ground and leaf litter combined ($t = 3.93$, df = 24, $P < 0.001$) were higher in invaded plots (Table 4.1).

When creating the variable representing the composition of tree species in the canopy, I accepted a two axes ordination (stress: 18.8, total variance explained: 83.9%, variation transferred to axes 1 and 2: 63.5% and 19.4% respectively) (Figure A.1). Box elder (*A. negundo*) was strongly negatively associated with NMDS axis 1 (Figure 4.2). Osage orange (*M. pomifera*) and Ohio buckeye (*A. glabra*) had a strong positive association with NMDS axis 2 while sugar maple (*Acer saccharum*) and American elm *U. americana*) showed a strong trend in the opposite direction (Figure 4.2). Because NMDS axis 1 explained the majority of the variation in the canopy tree community, I used the NMDS axis 1 ordination scores of each study plot as values for the canopy composition variable.

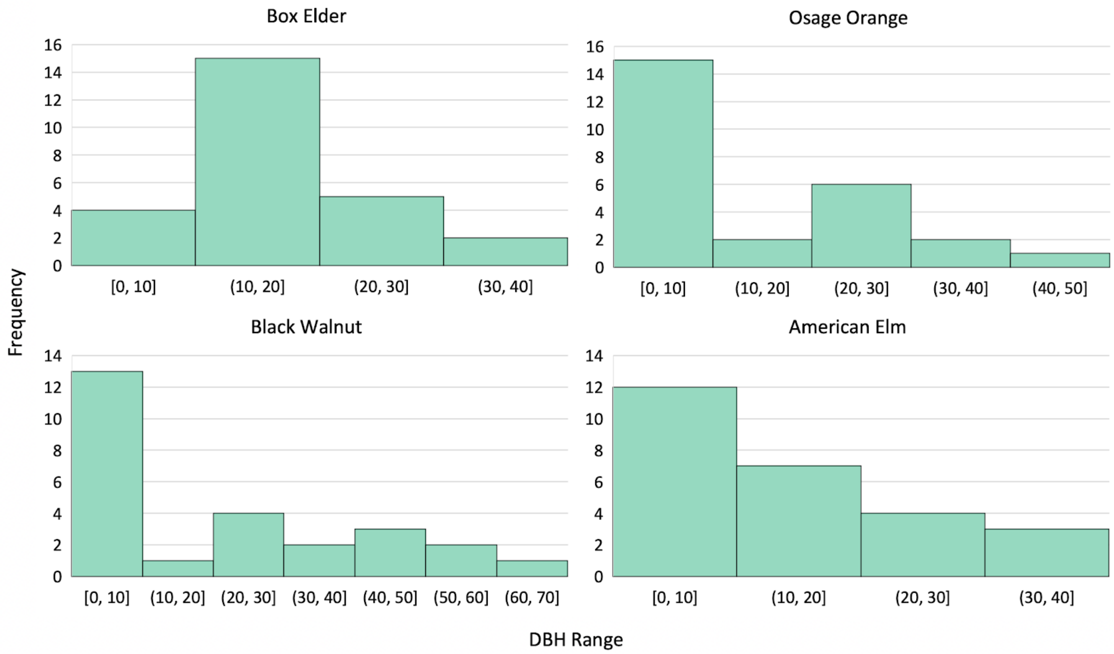

Figure 4.1. Distributions of the DBH (cm) of the four canopy species of trees most commonly observed over all plots; data collected in Greene County, OH along the Little Miami River during June - July 2019.

Table 4.1. Habitat attributes of plots and areas adjacent to the plots (n = 26); data collected in Greene County, OH along the Little Miami River during June - July 2019. Plot-bordering measures were only included in the calculations of plot-bordering means and standard deviations. Asterisk, "*", designates variables that differ significantly (*P* < 0.05) between plots invaded by and removed of honeysuckle.

Habitat parameter	Plot means (±SD)	Plot-bordering means (±SD)	Honeysuckle invaded plot means (±SD)	Honeysuckle removed plot means (±SD)
Canopy composition	0.00 (±0.25)	NA	0.05 (±0.32)	-0.02 (±0.22)
Frequency of snags (count)	2.58 (±3.34)	2.27 (±0.53)	5.00 (±5.07)	1.50 (±1.34)
Canopy cover (%)	84.94 (±7.64)	81.91 (±13.76)	84.90 (±5.87)	84.95 (±8.47)
Basal area (m^2/plot)	1.20 (±0.61)	1.03 (±0.56)	1.11 (±0.37)	1.25 (±0.70)
Canopy diversity (Shannon diversity score)	1.09 (±0.41)	1.10 (±0.46)	1.13 (±0.40)	1.07 (±0.43)
Canopy crown length (m)	9.37 (±1.97)	9.73 (±2.61)	8.77 (±1.94)	9.64 (±1.97)
Canopy height (m)	13.92 (±2.75)	15.20 (±3.18)	14.71 (±3.34)	13.58 (±2.47)
Understory cover (%)*	29.4 (±32.22)	32.77 (±29.05)	74.80 (±13.72)	9.22 (±6.90)
Understory invasive cover (%)*	25.17 (±34.01)	28.36 (±29.78)	73.58 (±15.33)	3.66 (±3.33)
Honeysuckle cover (%)*	24.34 (±34.25)	24.30 (±27.39)	73.11 (±15.33)	2.67 (±3.42)
Understory native cover (%)*	4.22 (±5.62)	4.41 (±4.95)	1.22 (±1.8)	5.56 (±6.25)
Understory diversity (Shannon diversity score)	0.31 (±0.44)	0.30 (±0.35)	0.19 (±0.42)	0.36 (±0.44)
Frequency of understory stems (count)*	31.38 (±48.40)	38.04 (±51.95)	88.75 (±53.48)	5.89 (±5.5)
Frequency of understory invasive stems (count)*	36.42 (±54.45)	40.08 (±50.78)	113.5 (±27.45)	2.17 (±3.42)
Frequency of honeysuckle stems (count)*	36.12 (±54.65)	35.81 (±50.33)	113.5 (±27.45)	1.72 (±3.46)
Frequency of understory native stems (count)	2.92 (±3.83)	3.27 (±5.10)	1.13 (±2.42)	3.72 (±4.11)
Forb groundcover (%)*	33.88 (±23.36)	39.36 (±27.01)	12.22 (±6.80)	43.51 (±21.55)
Bare and leaf litter groundcover (%)*	63.50 (±23.22)	57.73 (±29.47)	84.86 (±10.12)	54 (±20.99)
Logs/stumps groundcover (%)	1.60 (±1.50)	2.07 (±2.62)	1.50 (±1.36)	1.64 (±1.59)
Fern groundcover (%)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)
Woody plant groundcover (%)	2.29 (±1.92)	1.96 (±1.23)	2.59 (±1.98)	2.15 (±1.94)

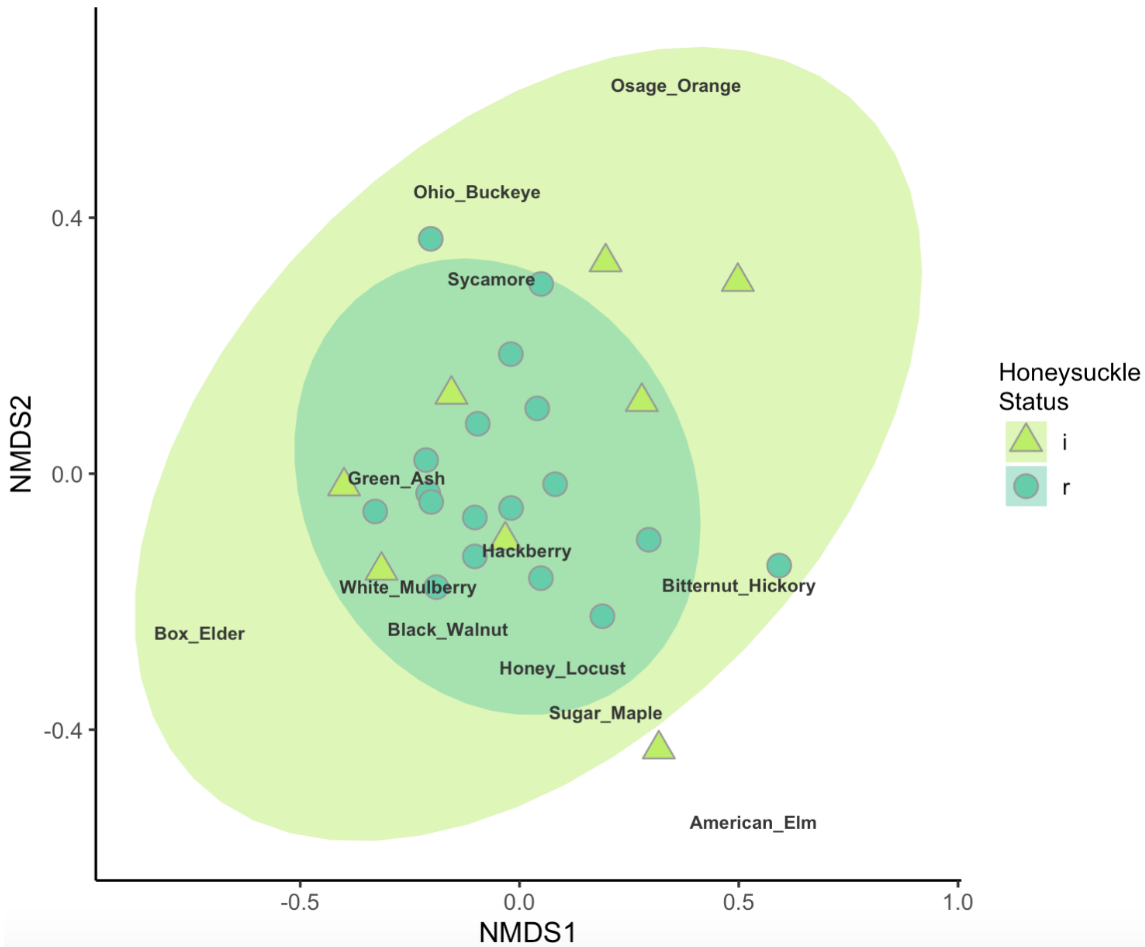

Figure 4.2. Ordination plot of canopy community composition where "i" (green triangles) represent plots invaded by honeysuckle, and "r" (turquoise circles) represent plots removed of honeysuckle; data collected in Greene County, OH along the Little Miami River during June - July 2019. Filled ovals are the 95% confidence interval ellipses of each category of plot honeysuckle status (invaded and removed).

Avian species

I observed 62 different avian species total - 59 in removed plots and 46 in invaded plots - over the course of my sampling efforts (for a list specifically of the species used in analysis, see Table A.1). Raw counts of these species showed that I observed 71% of species more frequently in honeysuckle removed plots than in honeysuckle invaded plots (Figure 4.3). Species such as the house wren (*Troglodytes aedon*), Acadian flycatcher, indigo bunting (*Passerina cyanea*), song sparrow (*Melospiza melodia*), blue-gray gnatcatcher (*Polioptila caerulea*), yellow-throated warbler (*Setophaga dominica*), and white-breasted nuthatch (*Sitta carolinensis*) showed raw count trends that suggest a positive response to removal (Table A.1); these species were 51-610% more numerous in removed plots, except for the blue-gray gnatcatcher (23% more numerous). The northern cardinal, rose-breasted grosbeak (*Pheucticus ludovicianus*), and red-eyed vireo appeared to show raw count trends in the opposite direction, being 24-82% more frequent in invaded plots (Table A.1).

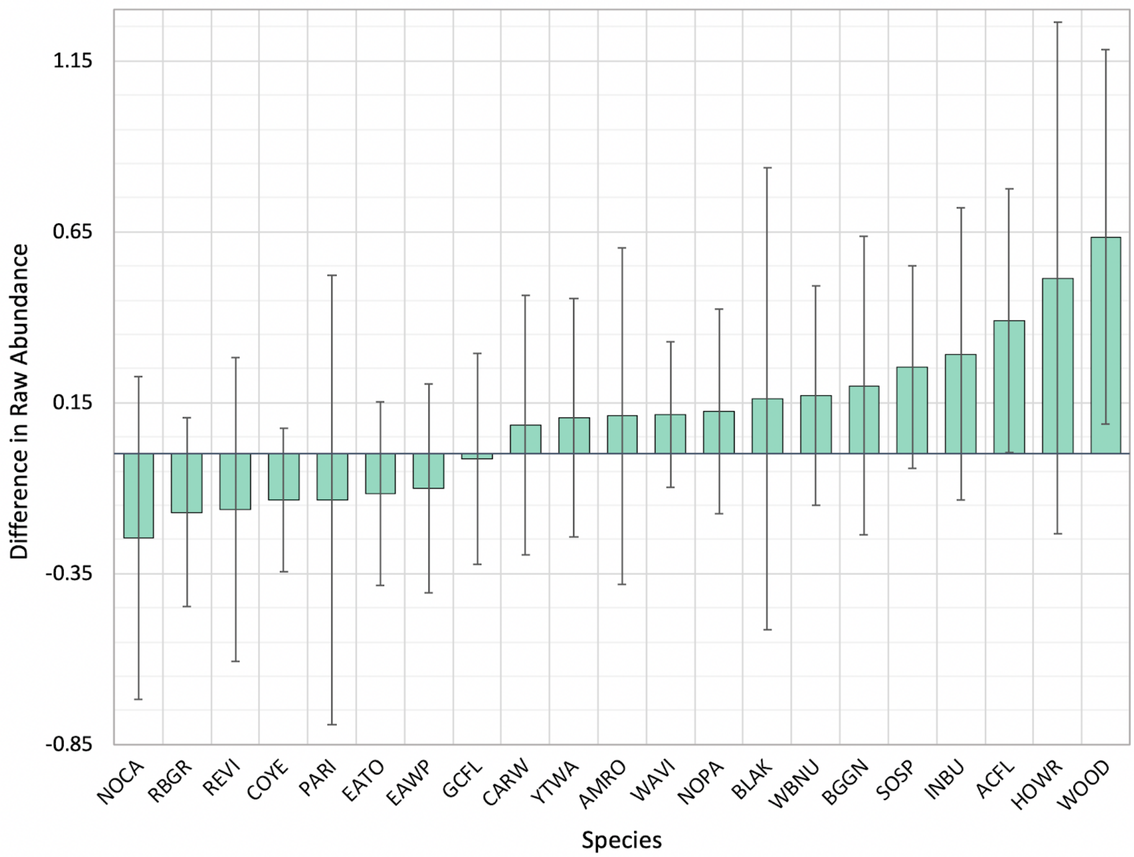

Figure 4.3. Average difference in raw counts between removed and invaded plots (removed minus invaded) across all plot visits – this only includes the species that I observed more than 10 times; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Error bars represent +/- 1 standard deviation. American Ornithological Society alpha banding codes represent the avian species (exceptions: BLAK = EUST and BHCO; PARI = CACH and TUTI; WOOD = NOFL, HAWO, DOWO, PIWO, RHWO, and RBWO - I combined these species to account for potential misidentifications).

Avian Community Composition

In total, 36 avian species met the criteria for inclusion in the NMDS ordination. I accepted a three axis ordination (stress: 16.7, total variance explained: 76.2%, variation transferred to axes 1, 2, and 3: 31.7%, 22.0%, and 22.3% respectively) (Figure A.2). The resulting ordination showed that plots invaded by honeysuckle seemed to group separately from plots removed of honeysuckle, however, there was some overlap between clusters of plots invaded by and removed of honeysuckle, particularly between NMDS axes 1 and 2. Invaded plots had more variation than removed plots, as demonstrated by 95% confidence interval ellipses - this is likely due to a smaller sample size of invaded plots. ANOSIM results suggest that there was a difference in avian community structure between plots invaded by vs. removed of honeysuckle ($P = 0.005$, R = 25.60).

In terms of habitat parameters, NMDS axis 3 displayed a strong gradient of honeysuckle invaded habitat and diversity of tree species in the canopy to honeysuckle-removed habitat (Figure 4.4). Honeysuckle cover and frequency of honeysuckle stems were strongly negatively associated with NMDS axis 3 ($P = 0.01$, $R^2 = 0.42$ and $P = 0.01$, $R^2 = 0.39$, respectively); diversity of tree species in the canopy showed a moderately negative trend ($P = 0.07$, $R^2 = 0.20$; Figure 4.4). Diversity of woody species in the understory, frequency of native woody stems in the understory, and crown length of trees in the canopy layer showed moderate trends in the opposite direction ($P = 0.08$, $R^2 = 0.20$, $P = 0.07$, $R^2 = 0.22$, and $P = 0.08$, $R^2 = 0.25$, respectively). NMDS axis 1 seems to be a gradient associated with honeysuckle found adjacent to plots with a somewhat strong correspondence with plot-bordering honeysuckle cover in the positive direction ($P =$

0.05, $R^2 = 0.30$; Figure 4.4). Although habitat parameters were associated with NMDS axis 2, their R^2 values and *P*-values were low and high respectively. There is arguably a weak gradient of forest habitat to snags, with many contributing variables on the forest habitat end of the gradient such as basal area of canopy trees and canopy tree height and cover. NMDS axis 2 likely represents the natural variation in avian communities found in rural riparian habitat.

With regard to avian species, woodpeckers and the Acadian flycatcher, white-breasted nuthatch, yellow-billed cuckoo (*Coccyzus americanus*), and yellow-throated warbler were strongly positively associated with NMDS axis 3 while the common yellowthroat (*Geothlypis trichas*), eastern-wood pewee, and eastern towhee showed the opposite relationship, but not as strongly (Figure 4.4). While no species in particular had a strong positive relationship with NMDS axis 1, the house wren, cerulean warbler (*Setophaga cerulea*), and indigo bunting as well as combined brown-headed cowbird and European starling were strongly negatively correlated with NMDS axis 1. The warbling vireo (*Vireo gilvus*), mourning dove (*Zenaida macroura*), great-crested flycatcher (*Myiarchus crinitus*), wood thrush, combined Carolina chickadee and tufted titmouse, red-winged blackbird (*Agelaius phoeniceus*), rose-breasted grosbeak, and gray catbird displayed a strong positive correspondence with NMDS axis 2 (Figure 4.4). However, the blue jay (*Cyanocitta cristata*) and eastern phoebe (*Sayornis phoebe*) were strongly negatively associated with NMDS axis 2. The American robin, Carolina wren (*Thryothorus ludovicianus*), and red-eyed vireo had strong associations, but with more than one axis: the American robin was negatively associated with NMDS axis 3 and positively associated with NMDS axis 2, the Carolina wren was positively associated with NMDS axis 3 and negatively with NMDS axis 2, and the red-eyed vireo was negatively associated with NMDS axes 2 and 3 (Figure 4.4).

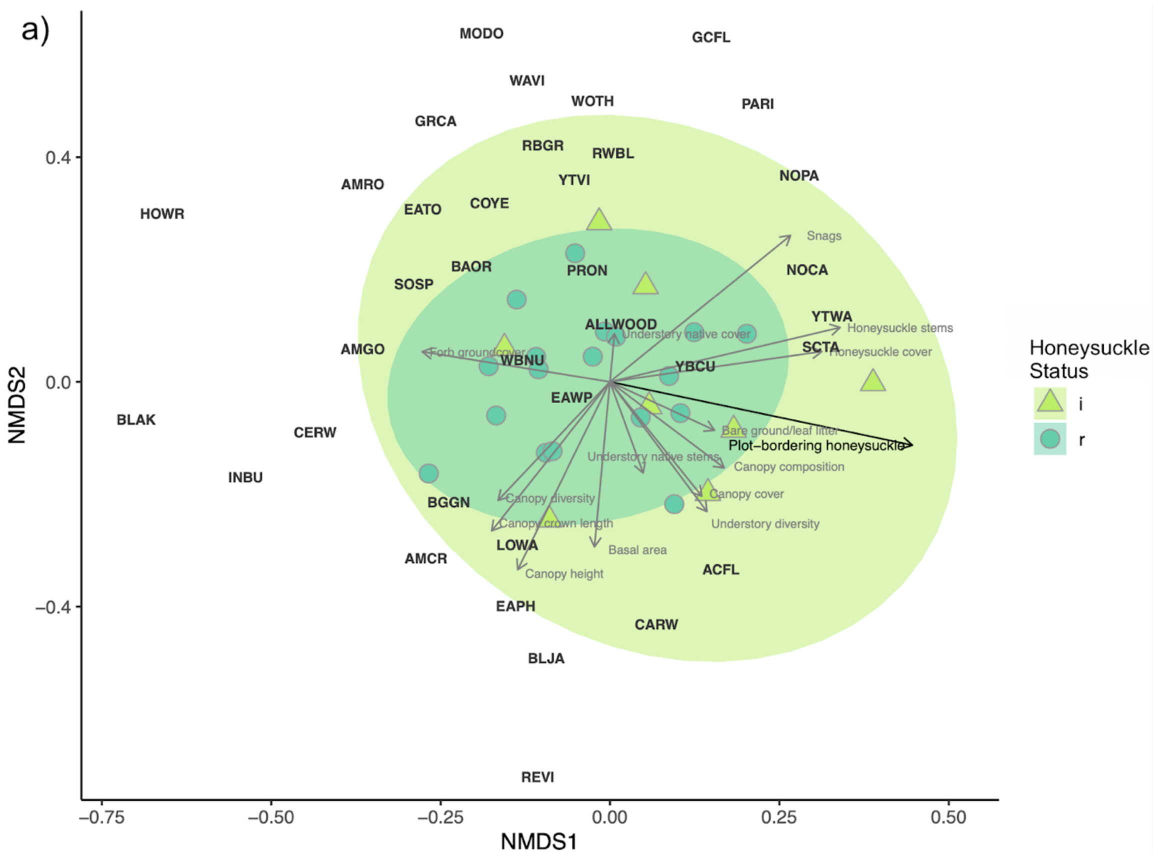

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Figure 4.4. 2-D ordination plots of all NMDS axis combinations: a) axis 1 and 2, b) axis 1 and 3, and c) axis 2 and 3. Where “i” (green triangle) represents plots invaded by honeysuckle and “r” (turquoise circle) represents plots removed of honeysuckle; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Filled ovals are 95% confidence interval ellipses of each category of plot honeysuckle status (invaded and removed). Black and grey arrows designate habitat parameter vectors with $R^2 \geq 0.2$ and $R^2 < 0.2$ respectively (length of arrows corresponds to correlation coefficients). American Ornithological Society alpha banding codes represent the 36 avian species included in the ordination (exceptions: BLAK = EUST and BHCO; PARI = CACH and TUTI; ALLWOOD = NOFL, HAWO, DOWO, PIWO, RHWO, and RBWO). For simplicity and ease of interpretation, I excluded some habitat parameters that were redundant with other variables or showed little association with the axes.

Figure 4.4 continued

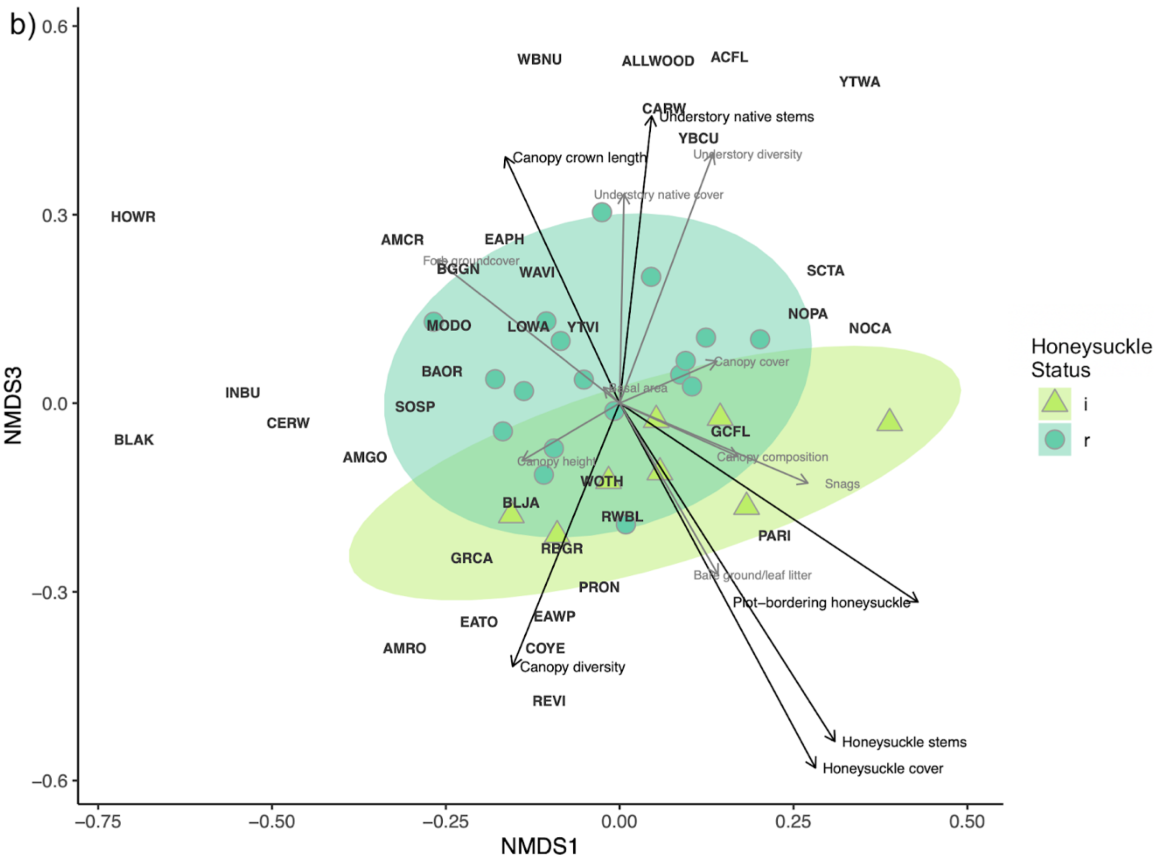

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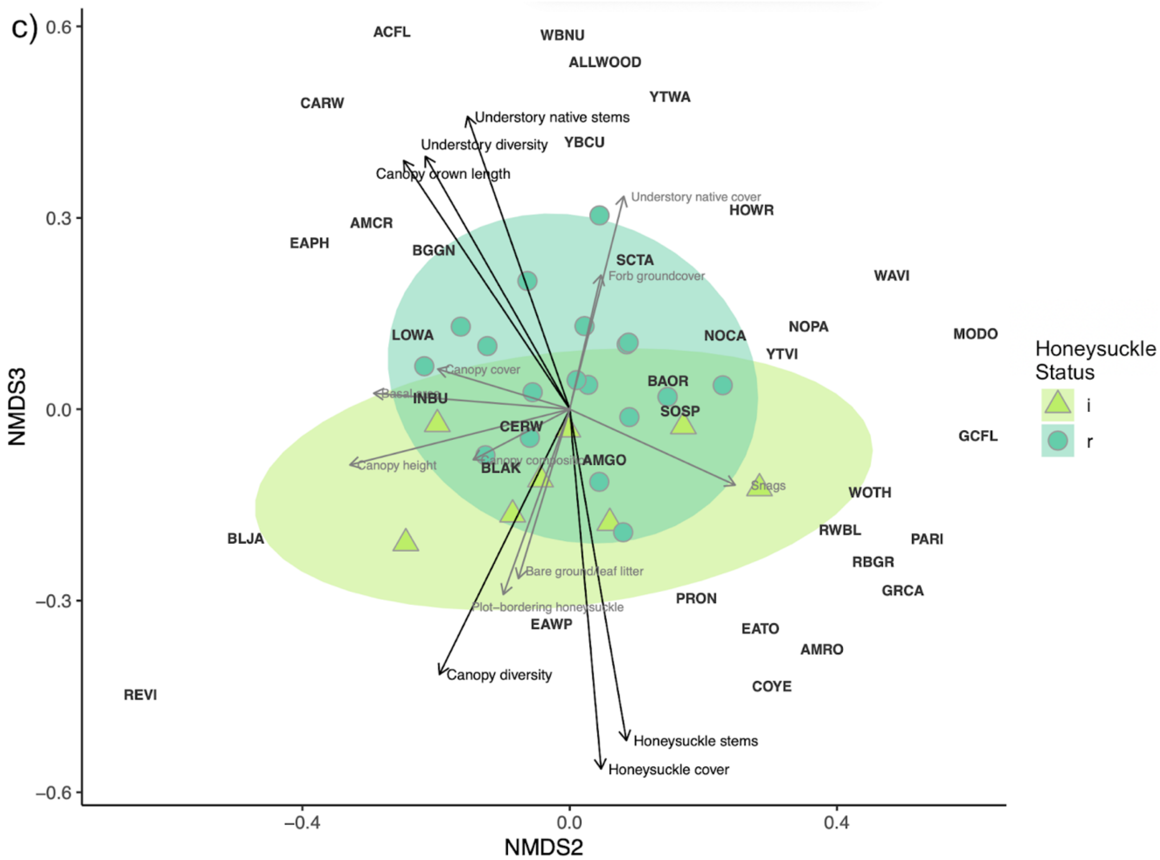
Figure 4.4 continued



Avian Species Abundance, Diversity, and Richness

The ten most frequently observed species, to be modeled using the candidate model set, were the Acadian flycatcher, American robin, blue-gray gnatcatcher, Carolina wren, house wren, indigo bunting, northern cardinal, northern parula (*Setophaga americana*), combined Carolina chickadee and tufted titmouse (combined to account for potential misidentification), and red-eyed vireo (Table A.1). Most of the top ten most commonly observed individual species did not respond to honeysuckle removal (Table 4.2). The only species that showed signs of an effect were the Acadian flycatcher and house wren. Honeysuckle removal had a moderately positive effect on Acadian flycatcher abundance (P=0.09, z = 1.70, second top-ranked model; Table 4.2). Most Acadian flycatcher models within 7 ΔAIC showed this trend to varying degrees. Level of invasion at invaded plots, i.e., honeysuckle cover, was slightly more important in terms of Acadian flycatcher abundance than honeysuckle status alone, ranking as the top model in the candidate set and also having a moderately strong negative effect (P = 0.06, z = -1.90; Table 4.2, Figure 4.5). Predicted Acadian flycatcher abundances suggest a 1.59-fold difference in abundance between plots invaded by vs. removed of honeysuckle (Figure 4.6, Table A.6). Evidence of honeysuckle removal effect on the house wren was not strong: only the deadwood model (ΔAIC = 2.6) showed a weak positive effect of honeysuckle removal on house wren abundance (P = 0.12, z = 1.55; Table 4.2, Table A.3). Model-averaged predictions showed a 0.7-fold difference between house wren abundance in removed vs. invaded plots (Figure 4.6, Table A.6). In addition to the weak within-plot honeysuckle effect, plot-bordering honeysuckle had a moderately negative effect on house wren abundance (*P* = 0.07, z = -1.845, top model).

Although most individual species were not impacted by honeysuckle status or cover, some responded to other habitat parameters. Various canopy measures had a moderately negative effect on American robin abundance: canopy cover (*P* = 0.08, z = -1.78) and crown length of canopy trees (*P* = 0.08, z = -1.75) in the American robin top model and basal area of canopy trees in the next two highest-ranking models (*P* = 0.09, z = -1.72 and *P* =0.03, z = -2.20, respectively) (Table 4.2, Table A.5). The northern parula responded strongly negatively to the basal area of canopy trees in its top two models (*P* = 0.03, z = -2.116 and *P* = 0.05, z = -1.96 respectively). Canopy cover had a weak negative effect on indigo bunting abundance (*P* = 0.12, z = -1.55, top model) (Table 4.2, Table A.5). The red-eyed vireo responded moderately positively to the basal area of canopy trees (*P* = 0.07, z = 1.83, top-ranked model). Null models for the house wren, indigo bunting, northern parula, and red-eyed vireo had a ΔAIC of less than two, but were not top models (Table 4.2, Table A.5). No habitat parameters were associated with the blue-grey gnatcatcher, Carolina wren, northern cardinal, or combined Carolina chickadee and tufted titmouse - null models were the top model for each of these species (Table 4.2, Table A.5).

With regard to species guilds and all species combined, honeysuckle removal had an effect on some groups but not others. Removal had a moderately positive effect on the abundance of all species combined (*P* = 0.07, z = 0.09, top model; Table 4.3). Most models with less than seven ΔAIC showed similar results (Table 4.3, Table A.3).

Woodpeckers responded strongly positively to honeysuckle removal (P = 0.003, z = 2.92, top model; Table 4.3). All models with less than seven ΔAIC showed this strong trend (Table 4.3,Table A.3). Honeysuckle removal showed a strong positive effect on species that prefer open woodland habitat (P = 0.05, z = 1.92, third top-ranked model; Table 4.3). All open woodland guild models with less than seven ΔAIC showed similar trends except for the top two models (Table 4.3, Table A.3). Abundance predictions for all species groups were unreliable due to low predicted detection probabilities (causing an unreasonable inflation of abundance predictions). Removal had no effect on long or resident-short distance migrants or shrub-nesters. Null models fell within two AIC of the top model for each of these three species groups and was the top model for both long distance migrants and shrub-nesters (Table 4.3).

Other habitat parameters had effects on the different groups of multiple species. Plot-bordering honeysuckle had a negative effect to some degree on the abundance of all species combined (P = 0.11, z = -1.60, second top-ranked model) and species preferring open woodland habitat (P = 0.11, z = -1.61, top model, P =0.009, z = -2.60, second top-ranked model), and a positive impact on woodpecker abundance (P =0.04, z = 2.01, top model; Table 4.3, Table A.5). The composition of tree species in the canopy had a moderately strong negative effect on the abundance of species that prefer open woodland habitat (P =0.08, z = -1.73, top model; Table 4.3, Table A.5). Basal area of canopy trees had a moderate to strong negative effect on the abundance of short-distance migrants (P = 0.03, z = -2.12, and P = 0.03, z = -2.15, top two models respectively) and all species combined (P = 0.06, z = -1.86, top model; Table 4.3, Table A.5). Abundance of species that prefer open woodland habitat responded weakly to strongly negatively to canopy cover ($P = 0.11$, $z = -1.62$, top model and $P = 0.01$, $z = -2.45$, third top-ranked model; Table 4.3, Table A.5).

The null model was a top model for both richness and diversity. Nevertheless, honeysuckle removal appeared to have a weak to moderately strong positive effect on both species richness and diversity (Table 4.4). Four of the seven top (ΔAICc < 2) richness models and two of the five top diversity models showed this result, i.e., species richness honeysuckle status ($P = 0.14$, $t = 1.53$), canopy crown length ($P = 0.08$, $t = 1.85$), basal area ($P = 0.11$, $t = 1.66$), and canopy cover ($P = 0.14$, $t = 1.54$) models and diversity canopy crown length ($P = 0.07$, $t = 1.87$) and basal area ($P = 0.14$, $t = 1.53$) models (Table 4.4). These models explained 13-17% and 8-20% of the variation in richness and diversity respectively (Table 4.4). Model averages predicted a 1.46-fold greater species richness and 0.1-fold greater Shannon diversity in honeysuckle-removed plots than invaded (Figure 4.7, Table A.6). Crown length and basal area of canopy trees both had weak negative effects on species richness ($P = 0.14$, $t = -1.53$ and $P = 0.14$, $t = -1.52$, respectively) (Table 4.4, Table A.5). Canopy crown length also had a weak negative effect on diversity ($P = 0.07$, $t = -1.88$) (Table 4.4, Table A.5).

Table 4.2. AIC table of the top N-mixture models (ΔAIC < 2) of the abundances of each of the top ten most commonly observed individual species as well as model fit statistics; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Coefficients for removed honeysuckle status are listed when applicable. Asterisks are next to removed plot estimates when the estimates of honeysuckle status have significance and next to model names when variables other than honeysuckle status are significant. "*" designates a weak effect if any ($P < 0.15$), "**" represents a moderate effect ($P < 0.10$), "***" designates a strong effect ($P < 0.05$). American Ornithological Society alpha banding codes designate the avian species (exception: PARI = CACH and TUTI).

Species	Model name	Removed plot estimate (±SE)	Negative log-likelihood	k	AIC	ΔAIC	Weight	Cumulative weight	SSE	Chisq	tukey
ACFL	Honeysuckle cover**	n/a	52.12	8	120.23	0.00	0.28	0.28	0.94	0.71	0.83
	Honeysuckle status	1.06 (±0.62)**	52.71	8	121.43	1.19	0.16	0.44	0.91	0.82	0.78
	Canopy crown length	0.91 (±0.63)	52.04	9	122.08	1.84	0.11	0.55	0.92	0.77	0.76
AMRO	Canopy**	n/a	51.19	7	116.38	0.00	0.32	0.32	0.81	0.73	0.61
	Reduced Canopy**	n/a	53.45	5	116.89	0.51	0.25	0.57	0.66	0.83	0.63
	Basal area***	0.09 (±0.51)	54.08	5	118.15	1.77	0.13	0.71	0.70	0.76	0.56
BGGN	Null	n/a	88.44	3	182.89	0.00	0.29	0.29	0.99	0.99	0.99
	Honeysuckle cover	n/a	88.12	4	184.23	1.34	0.15	0.44	0.99	0.99	0.99
	Honeysuckle status	0.23 (±0.34)	88.20	4	184.41	1.52	0.13	0.57	0.99	0.99	0.99
CARW	Null	n/a	66.33	3	138.66	0.00	0.27	0.27	0.86	0.95	0.79
	Reduced Canopy*	n/a	65.04	5	140.09	1.43	0.13	0.40	0.86	0.86	0.78
	Canopy crown length*	0 (±0.38)	65.12	5	140.24	1.58	0.12	0.53	0.86	0.85	0.78
	Honeysuckle cover	n/a	66.23	4	140.47	1.81	0.11	0.64	0.84	0.93	0.73
	Honeysuckle status	0.12 (±0.38)	66.27	4	140.55	1.89	0.11	0.74	0.84	0.92	0.71
HOWR	Plot-bordering honeysuckle**	0.19 (±0.39)	92.51	6	197.02	0.00	0.24	0.24	0.83	0.92	0.71
	Honeysuckle status	0.49 (±0.35)	94.17	5	198.35	1.33	0.13	0.37	0.77	0.86	0.65
	Null	n/a	95.26	4	198.53	1.51	0.11	0.49	0.75	0.80	0.61
	Honeysuckle cover	n/a	94.48	5	198.96	1.95	0.09	0.58	0.76	0.85	0.63
	Canopy crown length	0.42 (±0.35)	93.51	6	199.01	1.99	0.09	0.67	0.80	0.90	0.61
INBU	Canopy cover*	0.46 (±0.38)	67.78	7	149.56	0.00	0.19	0.19	0.87	0.92	0.78

Continued

Table 4.2 Continued

	Null	n/a	69.87	5	149.74	0.19	0.17	0.36	0.80	0.87	0.77
	Honeysuckle status	0.49 (±0.38)	68.97	6	149.94	0.38	0.15	0.51	0.83	0.91	0.72
	Honeysuckle cover	n/a	69.02	6	150.04	0.48	0.15	0.66	0.84	0.89	0.73
NOCA	Null	n/a	88.89	3	183.79	0.00	0.24	0.24	0.89	0.92	0.88
	Honeysuckle cover	n/a	88.38	4	184.77	0.98	0.15	0.39	0.91	0.91	0.88
	Honeysuckle status	-0.25 (±0.29)	88.53	4	185.06	1.28	0.13	0.52	0.91	0.90	0.87
	Canopy composition	-0.27 (±0.28)	87.70	5	185.41	1.62	0.11	0.63	0.92	0.94	0.89
NOPA	Basal area***	0.24 (±0.39)	62.32	5	134.63	0.00	0.27	0.27	0.96	1.00	0.89
	Reduced Canopy***	n/a	62.50	5	135.01	0.38	0.23	0.50	0.95	0.99	0.89
	Null	n/a	64.96	3	135.92	1.29	0.14	0.65	0.90	0.99	0.90
PARI	Null	n/a	96.59	3	199.18	0.00	0.26	0.26	0.40	0.35	0.20
	Honeysuckle status	-0.27 (±0.29)	96.16	4	200.33	1.15	0.14	0.40	0.35	0.34	0.15
	Honeysuckle cover	n/a	96.20	4	200.39	1.21	0.14	0.54	0.33	0.32	0.14
	Canopy composition	-0.21 (±0.29)	95.54	5	201.09	1.91	0.10	0.64	0.36	0.33	0.16
REVI	Basal area**	-0.46 (±0.4)	68.22	5	146.44	0.00	0.19	0.19	0.63	0.72	0.53
	Null	n/a	70.28	3	146.57	0.12	0.17	0.36	0.57	0.71	0.52
	Reduced Canopy*	n/a	68.49	5	146.99	0.54	0.14	0.50	0.57	0.67	0.40
	Honeysuckle status	-0.37 (±0.4)	69.86	4	147.72	1.28	0.10	0.60	0.61	0.73	0.50
	Canopy crown length	-0.5 (±0.41)	69.04	5	148.07	1.63	0.08	0.68	0.58	0.66	0.33
	Canopy composition	-0.28 (±0.41)	69.15	5	148.30	1.85	0.07	0.76	0.57	0.78	0.44

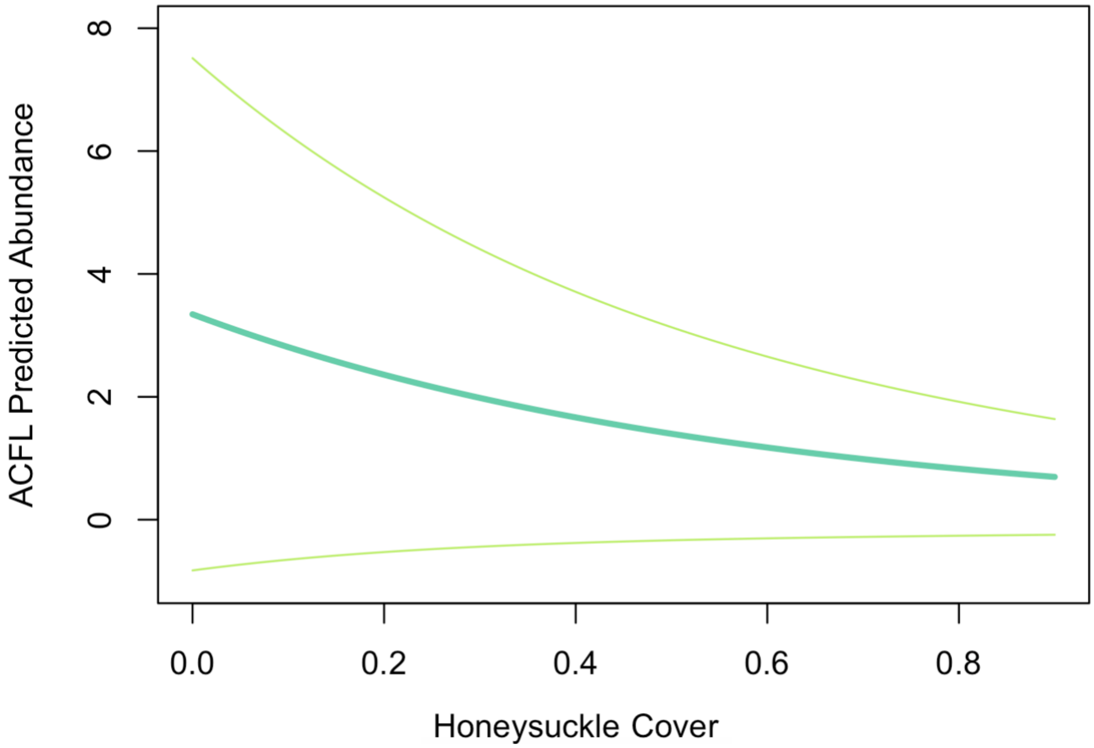


Figure 4.5. Relationship between the proportion of honeysuckle cover and the expected abundance of the Acadian flycatcher (turquoise line); data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Predictions are derived from the Acadian flycatcher top model. Green lines represent predicted standard error.

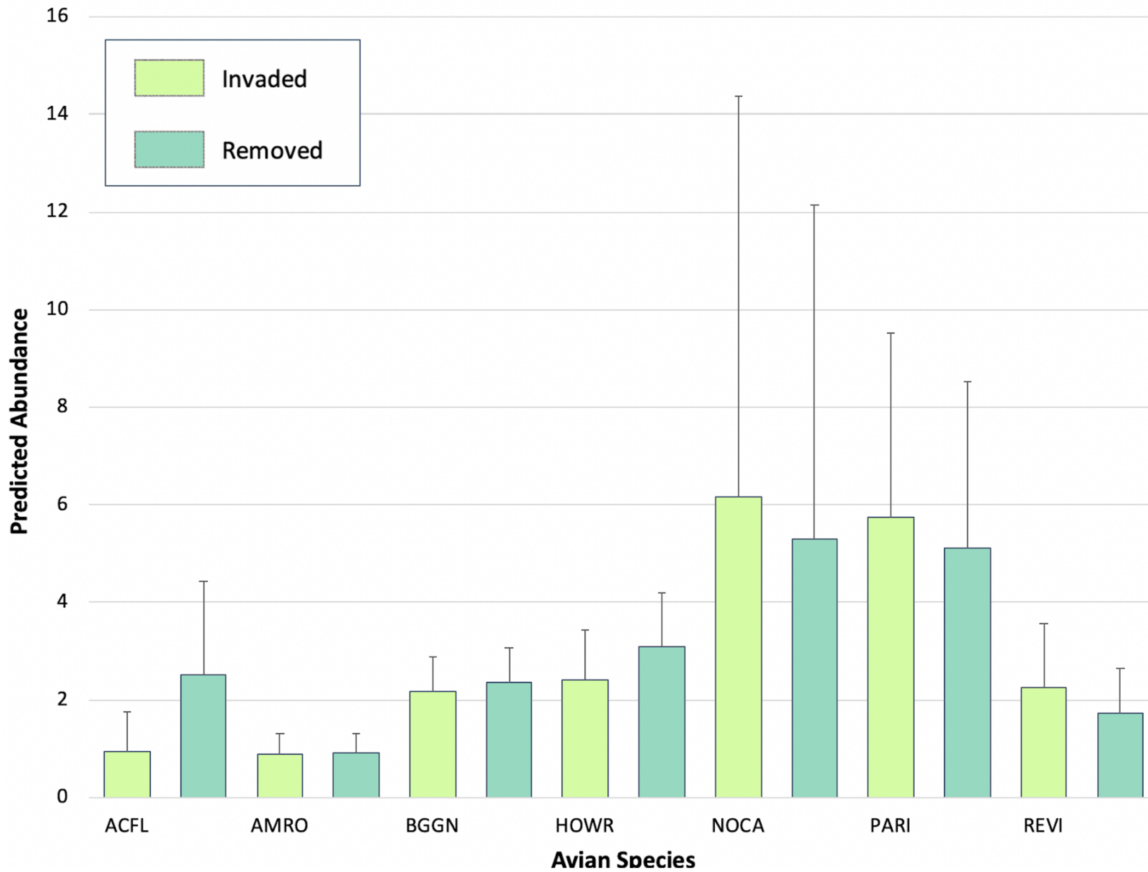


Figure 4.6. Expected avian abundance by honeysuckle status of seven of the ten most frequently observed species; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Predictions are derived from averaging top N-mixture models (ΔAIC < 2). Included are only those species of the ten which did not result in models with low detection predictions i.e. detection predictions of greater than 0.10. Error bars represent predicted standard error. American Ornithological Society alpha banding codes designate the avian species (exception: PARI = CACH and TUTI).

Table 4.3. AIC table of the top N-mixture models (ΔAIC < 2) of the abundances of species groups as well as model fit statistics; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Coefficients for removed honeysuckle status are listed when applicable. Asterisks are next to honeysuckle status estimates when estimates have significance and next to model names when variables other than honeysuckle status are significant. Single asterisk, "*", designates a weak effect if any ($P < 0.15$), "**" represents a moderate effect ($P < 0.10$), and "***" designates a strong effect ($P < 0.05$). ALL represents all species combined, LD = medium-long distance migrants, SD = resident-medium distance migrants, OW = species preferring open woodland habitat, WOOD = woodpeckers, and SN = shrub nesters.

Species	Model name	Removed plot estimate (±SE)	Negative log-likelihood	k	AIC	ΔAIC	Weight	Cumulative weight	SSE	Chisq	tukey
ALL	Basal area**	0.16 (±0.09)**	207.31	6	426.61	0.00	0.24	0.24	0.18	0.15	0.23
	Plot-bordering honeysuckle*	0.07 (±0.1)	207.76	6	427.52	0.91	0.15	0.39	0.18	0.13	0.21
SD	Basal area***	0.14 (±0.13)	162.26	5	334.53	0.00	0.24	0.24	0.79	0.76	0.82
	Reduced canopy***	n/a	162.53	5	335.07	0.54	0.18	0.42	0.80	0.79	0.82
	Null	n/a	164.89	3	335.79	1.26	0.13	0.54	0.65	0.59	0.71
	Plot-bordering honeysuckle*	0.02 (±0.15)	163.24	5	336.48	1.96	0.09	0.63	0.71	0.66	0.80
LD	Null	n/a	153.47	4	314.93	0.00	0.27	0.27	0.99	0.99	0.99
	Honeysuckle status	0.11 (±0.14)	153.14	5	316.27	1.34	0.14	0.41	0.98	0.99	0.99
	Honeysuckle cover	n/a	153.19	5	316.38	1.45	0.13	0.54	0.98	0.98	0.99
SN	Null	n/a	120.83	5	251.67	0.00	0.22	0.22	0.96	0.93	0.93
	Canopy composition**	-0.05 (±0.18)	119.02	7	252.05	0.38	0.18	0.40	0.97	0.97	0.96
	Honeysuckle cover	n/a	120.77	6	253.54	1.87	0.09	0.49	0.94	0.92	0.93
	Deadwood	0.03 (±0.19)	119.82	7	253.65	1.98	0.08	0.57	0.97	0.95	0.95
	Honeysuckle status	-0.02 (±0.19)	120.83	6	253.66	1.99	0.08	0.65	0.95	0.93	0.93

Continued

Table 4.3 Continued

OW	Global**	0.17 (±0.16)	154.47	11	330.93	0.00	0.35	0.35	0.84	0.76	0.94
	Plot-bordering honeysuckle***	0.09 (±0.16)	160.02	6	332.05	1.12	0.20	0.54	0.53	0.51	0.80
	Canopy cover***	0.27 (±0.14)***	160.40	6	332.81	1.88	0.14	0.68	0.60	0.55	0.83
WOOD	Plot-bordering honeysuckle***	1.04 (±0.35)***	92.46	6	196.92	0.00	0.38	0.38	0.34	0.59	0.26
	Honeysuckle cover***	n/a	94.41	5	198.82	1.90	0.15	0.53	0.25	0.49	0.18

Table 4.4. AIC table of the top GLMs (ΔAIC < 2) of species richness and Shannon diversity; data collected in Green County, OH during the 2019 peak breeding season. Coefficients for removed honeysuckle status are listed when applicable. Asterisks are next to honeysuckle status estimates when estimates have significance and next to model names when variables other than honeysuckle status are significant. Single asterisk, "*", designates a weak effect if any ($P < 0.15$), "**" represents a moderate effect ($P < 0.10$), and "***" designates a strong effect ($P < 0.05$).

	Model names	Removed plot estimate (±SE)	K	AICc	ΔAICc	AICc Weight	Log-likelihood	Cumulative weight	R^2
Richness	Null	n/a	2	139.96	0.00	0.17	-67.72	0.17	0.00
	Honeysuckle status	2.11 (±1.38)*	3	140.11	0.16	0.16	-66.51	0.33	0.09
	Canopy crown length*	2.55 (±1.37)**	4	140.41	0.46	0.14	-65.25	0.47	0.17
	Basal area*	2.24 (±1.35)*	4	140.45	0.49	0.14	-65.27	0.61	0.17
	Plot-bordering honeysuckle	1.1 (±1.54)	4	140.82	0.87	0.11	-65.46	0.72	0.16
	Canopy cover	2.12 (±1.38)*	4	141.58	1.63	0.08	-65.84	0.79	0.13
	Honeysuckle cover	n/a	3	141.61	1.66	0.08	-67.26	0.87	0.03
Diversity	Canopy crown length*	0.14 (±0.08)**	4	-9.75	0.00	0.23	9.83	0.23	0.20
	Null	n/a	2	-9.25	0.50	0.18	6.89	0.41	0.00
	Honeysuckle status	2.11 (±1.38)	3	-8.83	0.92	0.15	7.96	0.56	0.08
	Basal area	0.12 (±0.08)*	4	-7.81	1.94	0.09	8.86	0.64	0.14

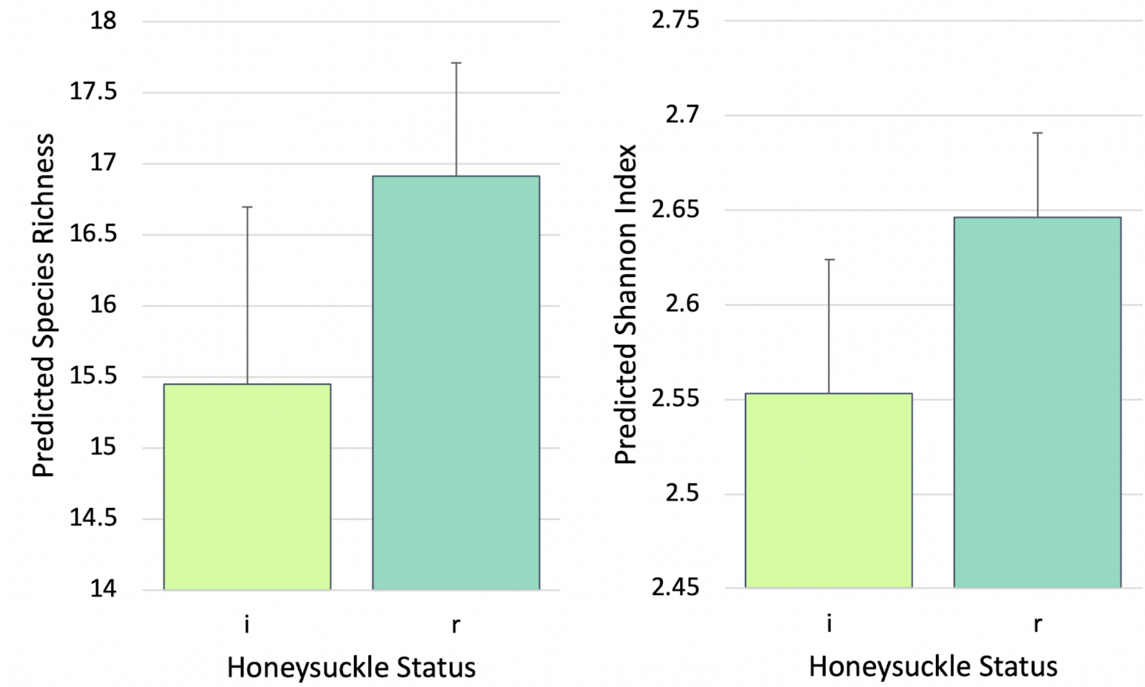


Figure 4.7. Species richness and Shannon diversity predicted means, i.e., expected values derived from averaging top GLMs (ΔAICc < 2), where "i" (green) represents plots invaded by honeysuckle and "r" (turquoise) represents plots removed of honeysuckle; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Error bars represent predicted standard error.

Chapter 5: Discussion

Vegetation

In order to advance as well as optimize honeysuckle management strategies, a better understanding of how removal affects avian community structure is required. This study took a step towards discerning the implications of honeysuckle removal on avian species in rural riparian forests. Habitat in plots removed of honeysuckle showed differences in vegetation structure and composition four to six years later when compared to plots invaded by honeysuckle. Removed plots contained little if any honeysuckle, confirming the effectiveness of the honeysuckle management strategies implemented. I found higher amounts of forb groundcover, and, correspondingly, lower levels of combined bare and leaf litter groundcover in plots removed of honeysuckle. These findings are congruent with past research. Studies have characterized vegetation growth underneath honeysuckle as less dense (Collier et al. 2002, Hartman and McCarthy 2008) and have documented the resurgence of herbaceous groundcover at least five years post-honeysuckle removal - likely due to the resulting open understory that does not shade out the plants below (Gould and Gorchov 2000). Honeysuckle removal can also result in the regeneration of native woody species at least five years later, likely as a result of less competition and shading (Runkle et al. 2007, Boyce 2015, Hopfensperger et al. 2019). Although understory native woody cover was greater in removed plots in the study, the 4.34% difference in means is likely not biologically significant (Table 4.1). My observations presumably represent the beginning of the regeneration of native understory plants in removed plots four to six years post-removal. It is possible that this study occurred too soon after honeysuckle removal for substantial differences between the amount of native understory in removed vs. invaded plots to be shown. More research is needed to determine the length of time that it takes post-honeysuckle removal for habitat to reach a state where restoration goals are met.

In turn, bird communities may be impacted differently when a habitat reaches this state than immediately post-honeysuckle removal. In the long-term, as the understory regenerates, the habitat might become less suitable for some species, e.g., overstory species that prefer a more open habitat. In the short term, stripping habitat completely of the shrub layer might discourage other species, e.g., shrub-nesters, from using the area until the understory develops to some extent (McCusker et al. 2010). Supplementing honeysuckle-removal with replacement-plantings of native shrubs or deer exclusion fences may promote quicker native understory development and thus weaken short-term negative impacts of removal on birds by, e.g., providing replacement food resources during the non-breeding season (McCusker et al. 2010, Simmons 2016, Haffey and Gorchov 2019). Removing honeysuckle in a stepwise, interspersed manner - temporarily maintaining the structural complexity that shrub species need while over the years increasingly creating matrix areas of removal for native regeneration to occur - might also prove to be an effective strategy for removing honeysuckle while mitigating short-term impacts to birds (Valente et al. 2019). Eradication strategies that involve either leaving dead shrubs standing or dense shrub debris behind may help alleviate immediate negative impacts to avian species in terms of providing structurally sheltering spaces in the fall and winter while also preventing deer browse and thus promoting the regrowth of some native woody species (Gorenzel et al. 1995, Lash 2018).

Avian Species

Avian Community Composition

I found that honeysuckle removal shapes the patterns of avian assemblage composition in rural riparian areas. The NMDS ordination suggests that plot-bordering honeysuckle and honeysuckle status explained the variation in avian community structure in addition to the natural variation found in avian communities in rural riparian areas. Some avian species were strongly associated with the gradient of honeysuckle invaded to removed habitat, with the Acadian flycatcher, white-breasted nuthatch, yellow-throated warbler, Carolina wren, and woodpeckers associated more with the honeysuckle-removed habitat end of the gradient. This group represents common riparian forest birds that use different structural dimensions. The red-eyed vireo, on the other hand, was associated with the honeysuckle-invaded habitat end of the gradient. All of these results correspond with my findings regarding raw species counts and percent greater frequency of individual species in removed plots. Interestingly, other studies have found the white-breasted nuthatch, yellow-throated warbler, carolina wren, and red-eyed vireo showing a wide range of and often conflicting responses to honeysuckle presence (McCusker et al. 2010, Lynch 2016).

Past research that occurred in Ohio has demonstrated a negative association between honeysuckle presence and the Acadian flycatcher (Rodewald 2005, Bakermans and Rodewald 2006, Rodewald 2009, Rodewald 2012b). The positive association that I observed between this species and honeysuckle removal is likely due to changes in habitat that correspond with Acadian flycatcher habitat preferences, i.e., lower amounts of understory density and thus a greater amount of space available for efficient aerial foraging (Wilson and Cooper 1998, Whitehead and Taylor 2002). On the other hand, the eastern wood-pewee, a species that has in multiple studies demonstrated trends similar to the Acadian flycatcher presumably for the same reasons (Wilson et al. 1995, Rodewald and Smith 1998, McCusker et al. 2010, Rodewald 2012b, Lynch 2016), appeared to show the opposite tendency in my study system, potentially because it is generally less associated with riparian areas (Billerman et al. 2020).

Previous studies somewhat support my findings regarding woodpeckers. McCusker et al. (2010) found that the red-bellied woodpecker (*Melanerpes carolinus*) preferred habitat that was not invaded by honeysuckle. It is possible that woodpeckers find honeysuckle presence obstructive to their foraging habits, i.e., bark-foraging (pileated woodpecker, downy woodpecker, *Dryobates pubescens*, hairy woodpecker, *Dryobates villosus*, and red-bellied woodpecker) or fly-catching (red-headed woodpecker, *Melanerpes erythrocephalus*), and hence the positive association of woodpeckers to honeysuckle removal in this study (Billerman et al. 2020). In terms of the northern flicker in particular, it is possible that the removal of honeysuckle created a more favorable groundlayer habitat for ground-foraging (Wiebe and Moore 2020).

Identifying the strong first axis of the NMDS, which was not influenced by plot-level variables, allowed for the ability to examine these responses of the community to honeysuckle removal. The fact that plot-bordering honeysuckle seemed to play a large role in explaining the variation of the avian community found in these data suggests that something on a broader scale is having a large influence. The house wren and combined brown-headed cowbird and European starling showed a negative association along a gradient of increasing plot-bordering honeysuckle in the NMDS ordination. Findings regarding raw species counts and percent greater frequency of individual species in removed plots of these species suggest a negative response to honeysuckle-invaded vs. removed plots as well. Previous studies show no association of honeysuckle presence with any of these species (McCusker et al. 2010, Rodewald 2012b, Lynch 2016). Observed avian individuals may have had territories that overlapped with the area adjacent to plots, opposite of the river (where the 50m point count radii extended outside of the plot; Figure 3.2). It is possible that a greater area of removed honeysuckle is needed for influences on certain species to occur. Future studies should consider using larger plots to assess the impact of honeysuckle removal on avian species and/or incorporate broader-scale habitat factors in the data collection and analysis.

Avian Species Abundance, Diversity, and Richness

Abundances of the Acadian flycatcher, woodpeckers, all species combined, and species that prefer open woodland habitat showed a promising positive response to honeysuckle removal almost ubiquitously across their top models. Both the Acadian flycatcher and woodpeckers were particularly sensitive in a negative way to the level of honeysuckle invasion in invaded plots. Species that prefer open woodland habitat were likely responding to the reduction of understory in removed plots - this result aligns with previous study findings that canopy species tend to avoid honeysuckle invaded areas (Rodewald 2005, McCusker et al. 2010, Lynch 2016). In terms of species richness and diversity, honeysuckle removal seemed to be influential, to have some positive biological relevance despite high-ranking null models; though this conclusion should be taken with caution. It is also worth noting that I observed the cerulean warbler only at removed plots (n = 5) and the wood thrush 73% more frequently in invaded plots (n = 8) - both species are in decline: vulnerable and near threatened respectively according to the IUCN Red List. For species richness, woodpeckers, all species combined, and species that prefer open woodlands, plot-bordering honeysuckle seemed to be a major factor at play. This further supports the aforementioned implications regarding the importance of plot-bordering honeysuckle in this study.

Findings regarding the impact of honeysuckle removal on the abundance of the Acadian flycatcher and woodpeckers align well with NMDS ordination results, i.e., results at the community-level corresponded with those at the species-level. Other species-level analysis did not correspond with NMDS results. I saw community-level responses from the Carolina wren and red-eyed vireo that did not translate to the species-level, i.e., abundance models showed no signs of an effect of honeysuckle removal. This demonstrates the importance of evaluating both individual species and community level patterns as they represent different ecological levels of organization. Future studies should consider multiscale implications when assessing restoration initiatives.

Honeysuckle removal did not appear to have a negative effect on some of the species and species groups which I expected it would, namely the American robin, northern cardinal, resident-short distance migrants, and shrub-nesters. However, other important types of avian species responses may show different trends. For example, researchers have found that nests built in honeysuckle by the American robin and northern cardinal experience higher levels of predation leading to lowered success (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Rodewald et al. 2010). Thus, even though the abundance of certain species in this study were not impacted by honeysuckle removal, the fecundity of these species could show different trends. Furthermore, certain avian species may be negatively impacted by honeysuckle removal during the non-breeding season, as, during the fall and winter, honeysuckle is structurally sheltering and provides an abundance of berries (Gleditsch and Carlo 2011). In order to more fully understand the implications of honeysuckle removal with regard to birds, aspects like fecundity, post-fledgling success, and avian use of honeysuckle-removed areas during different seasons of the year must be explored.

Studies examining the effect of honeysuckle removal in urban areas did not find differences in individual avian species abundances between invaded and removed sites, but did find differences between urban vs. rural sites (Rodewald 2016). Honeysuckle removal in rural areas may function differently than removal in urban areas, as it seems I have found. Rural areas tend to have less honeysuckle invasion than their urban counterparts (Borgmann and Rodewald 2005, White et al. 2014), and a different composition of avian communities (Croci et al. 2008, Rodewald 2012b, Evans et al.

2018). Considering that the abundance of resident-short vs. long distance migrants was not affected by honeysuckle removal in this study, it is possible that the previously documented differences in the honeysuckle presence preferences of these groups (Rodewald 2005) are more pronounced in urban spaces. Further research comparing urban to rural honeysuckle removal is needed to confirm these conclusions.

Limitations

The trends I observed may only be associated with local abundances of avian species. The small sample size of plots (particularly invaded plots), number of years of data collection (one), and geographic area restricts the broader assumptions that can be made with my findings regarding avian species. Although I surveyed and analyzed plots that are invaded by honeysuckle, I did not survey removed plots before honeysuckle removal occurred, an additional factor limiting the ability to extrapolate these results to the larger population. Furthermore, because some of my research plots bordered each other, the locations of point counts may not have been entirely independent of each other. It is possible that avian species observed on the fringes of point count 50m radii on the lengthwise ends of plots have territories that overlap with the fringes of adjacent point count location radii.

The prevalence of high-ranking null models (i.e., ΔAIC < 2) in my abundance, richness and diversity analysis may render some of my findings inconclusive. High-ranking null models suggest that it is likely that a large portion of the data pattern is due to random chance or unmeasured processes. Thus, in many cases, the data may not have been explained well by the variables included in the candidate model set. It is also possible that there was an impact in some cases where there appeared to be none - obscured by a small sample size paired with more-complicated and “data-hungry” model types.

Chapter 6: Conclusion

The goal of this study was to determine if and how removing honeysuckle impacts the structure of avian communities in rural areas. In particular, I investigated how avian community composition, abundance, richness, and diversity differed during the 2019 breeding season between plots within riparian habitat in Greene County, OH that were either removed of honeysuckle four to six years ago or invaded by honeysuckle. I found substantial habitat development in the herbaceous layer post-honeysuckle removal, but not necessarily in the shrub layer, where the native woody plants seemed to be only beginning to regenerate. Avian community structure differed between plots invaded by and removed of honeysuckle. Honeysuckle removal had a positive effect on the abundance of the Acadian flycatcher, woodpeckers, species that prefer open woodland habitat, and all species combined. The abundance of the American robin, blue-gray gnatcatcher, Carolina wren, indigo bunting, northern cardinal, northern parula, combined tufted titmouse and Carolina chickadee, and red-eyed vireo, and the following species guilds were not impacted by honeysuckle removal: shrub-nesters, resident-short distance migrants, and medium-long distance migrants. Species richness and diversity may have been positively influenced by honeysuckle removal, but this effect was less clear.

Overall, this study provides evidence that, after four to six years and in small plot sizes, honeysuckle removal in rural riparian areas can change avian community composition, particularly in terms of increasing the abundances of certain species and species groups, e.g., those that prefer forests with open understories. This suggests that managers can achieve conservation gains with even small land management efforts.

Future research should investigate the impact on avian species of different honeysuckle management techniques - e.g., supplementing removal with native woody plantings or deer exclusion fences, stepwise, interspersed removal, or leaving dead shrubs standing or in brush piles - and amounts of time since management. To gain a more complete understanding of how honeysuckle management affects avian species, future studies must also explore other avian response indicators, e.g., fecundity, post-fledgling success, and use of honeysuckle-removed areas during migration and winter months. Furthermore, because the amount of plot-bordering honeysuckle was important in this study system, researchers should consider using larger areas of honeysuckle removal and/or incorporating broader-scale habitat factors in similar future studies. This study provides a vital starting point for understanding the effects of honeysuckle removal on avian species particularly in rural riparian areas. Recognizing these effects paves the way toward optimizing management strategies and mitigating impacts to birds.

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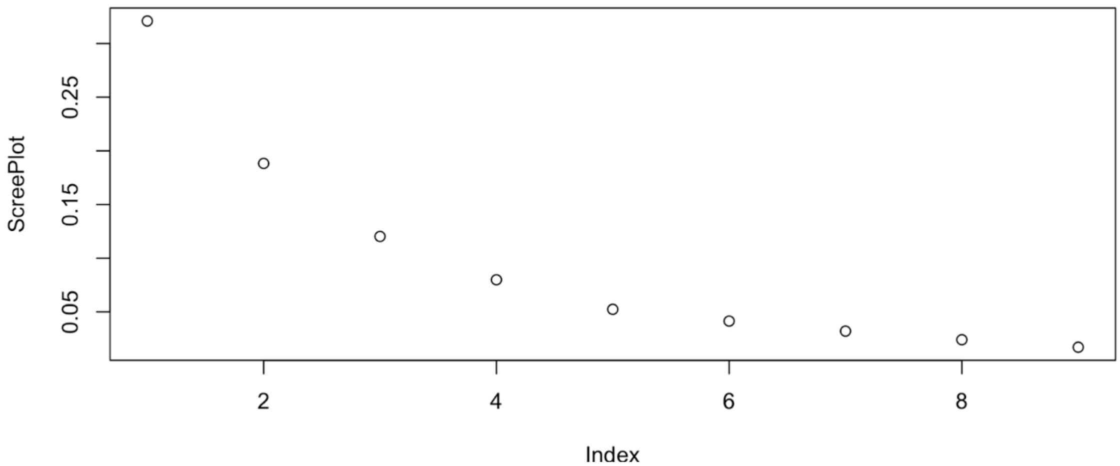
Appendix A: Supplemental Materials

a)



b)

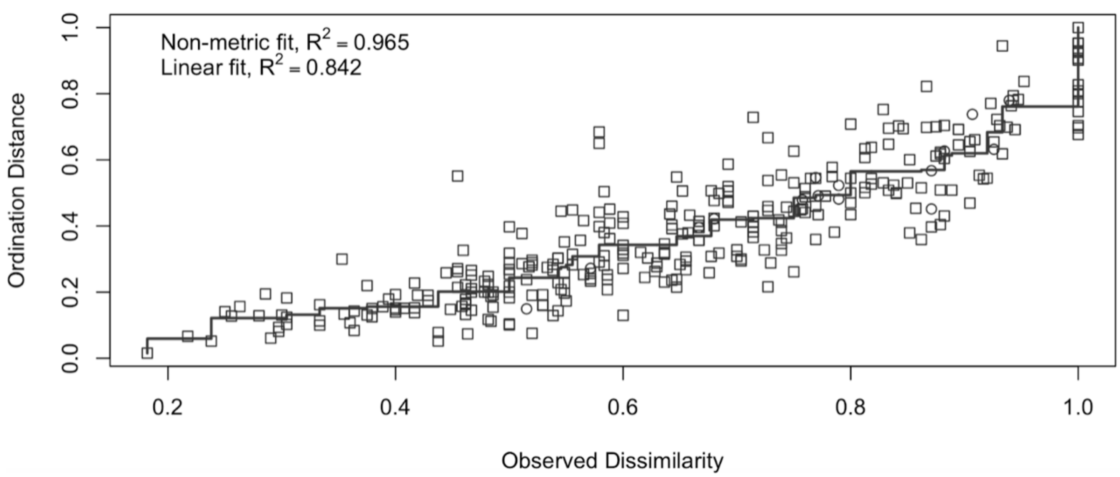


Figure A.1. Community composition of canopy trees a) scree-plot of NMDS stress values as the number of NMDS axes increases and b) Shepard diagram; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season.

Table A.1. Number of observations across all plots and average observations per plot type of all species used in data analysis; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. American Ornithological Society alpha banding codes designate the avian species (exceptions: BLAK = EUST and BHCO; PARI = CACH and TUTI; WOOD = NOFL, HAWO, DOWO, PIWO, RHWO, and RBWO - I combined these species to account for potential misidentifications).

Code	Common name	Scientific name	Total observations (n = 26)	Average observed in invaded plots (n = 8)	Average observed in removed plots (n = 18)
ACFL	Acadian flycatcher	*Empidonax virescens*	38	0.17	0.56
AMGO	American goldfinch	*Spinus tristis*	5	0.04	0.07
AMRO	American robin	*Turdus migratorius*	37	0.33	0.44
BAOR	Baltimore oriole	*Spinus tristis*	5	0.04	0.06
BGGN	Blue-gray gnatcatcher	*Polioptila caerulea*	87	0.88	1.07
BLAK	Brown-headed cowbird, European starling	*Baeolophus bicolor, Poecile carolinensis*	85	0.88	1.04
BLJA	Blue jay	*Cyanocitta cristata*	8	0.17	0.07
CARW	Carolina wren	*Thryothorus ludovicianus*	37	0.42	0.50
CERW	Cerulean warbler	*Setophaga cerulea*	5	0.00	0.09
COYE	Common yellowthroat	*Geothlypis trichas*	10	0.21	0.07
EABL	Eastern Bluebird	*Sialia sialis*	1	0.00	0.02
EAPH	Eastern phoebe	*Sayornis phoebe*	2	0.00	0.04
EATO	Eastern towhee	*Pipilo erythrophthalmus*	11	0.21	0.09
EAWP	Eastern wood-pewee	*Contopus virens*	28	0.42	0.31
FISP	Field sparrow	*Spizella pusilla*	1	0.00	0.02
GCFL	Great crested flycatcher	*Myiarchus crinitus*	28	0.29	0.28
GRCA	Gray catbird	*Dumetella carolinensis*	7	0.17	0.06
HOWR	House wren	*Troglodytes aedon*	95	0.71	1.22
INBU	Indigo bunting	*Passerina cyanea*	53	0.38	0.67

Continued

Table A.1. Continued

LOWA	Louisiana waterthrush	*Parkesia motacilla*	3	0.00	0.06
MODO	Mourning dove	*Zenaida macroura*	6	0.08	0.07
NOCA	Northern cardinal	*Cardinalis cardinalis*	73	1.04	0.80
NOFL	Northern flicker	*Colaptes auratus*	6	0.00	0.09
NOPA	Northern parula	*Setophaga americana*	36	0.38	0.50
PARI	Carolina chickadee, tufted titmouse	*Poecile carolinensis, Baeolophus bicolor*	74	1.00	0.87
PIWO	Pileated woodpecker	*Dryocopus pileatus*	5	0.04	0.06
PRON	Prothonatary warber	*Protonotaria citrea*	5	0.04	0.06
RBGR	Rose-breasted grosebeak	*Pheucticus ludovicianus*	10	0.21	0.04
REVI	Red-eyed vireo	*Vireo olivaceus*	46	0.63	0.46
RTHU	Ruby-throated hummingbird	*Archilochus colubris*	2	0.00	0.04
RWBL	Red-winged blackbird	*Agelaius phoeniceus*	2	0.08	0.00
SCTA	Scarlet tanager	*Piranga olivacea*	7	0.04	0.09
SOSP	Song sparrow	*Melospiza melodia*	20	0.04	0.30
WAVI	Warbling vireo	*Vireo gilvus*	17	0.13	0.24
WBNU	White-breasted nuthatch	*Sitta carolinensis*	22	0.13	0.30
WOOD	Downy woodpecker, hairy woodpecker, northern flicker, pileated woodpecker, red-bellied woodpecker, red-headed woodpecker	*Dryobates pubescens, Dryobates villosus, Colaptes auratus, Dryocopus pileatus, Melanerpes carolinus, Melanerpes erythrocephalus*	64	0.42	0.94
WOTH	Wood thrush	*Hylocichla mustelina*	8	0.21	0.06
YBCU	Yellow-billed cuckoo	*Coccyzus americanus*	6	0.08	0.07
YEWA	Yellow warbler	*Setophaga petechia*	1	0.00	0.02
YTVI	Yellow-throated vireo	*Vireo flavifrons*	6	0.04	0.09
YTWA	Yellow-throated warbler	*Setophaga dominica*	23	0.21	0.31

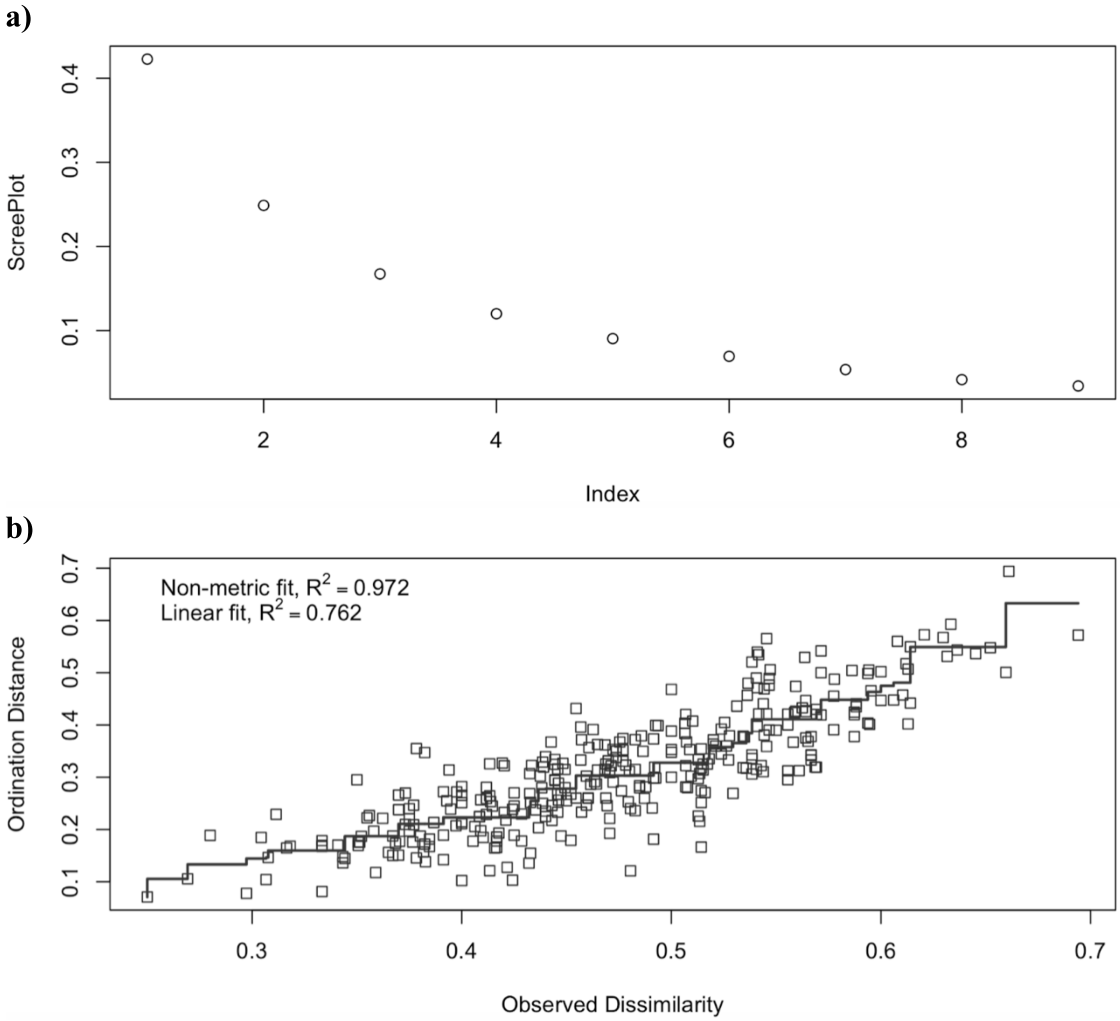


Figure A.2. Community composition of avian species a) scree-plot of NMDS stress values as the number of NMDS axes increases and b) Shepard diagram; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season.

Table A.2. N-mixture model AIC table of the top detection functions (ΔAIC < 2) of the abundance models; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Null (k = 2) and global models (k = 8) are also listed regardless of whether they were a top model; null models represented as "~1 ~ 1" and global models as "~date + time + noise + temp + wind + clouds ~ 1." American Ornithological Society alpha banding codes designate the avian species (exception: PARI = CACH and TUTI). ALL = all species combined, LD = medium-long distance migrants, SD = resident-medium distance migrants, OW = species preferring open woodland habitat, WOOD = woodpeckers, and SN = shrub nesters. Date = days since first point count, time = time of day, noise = noise level, temp = temperature, cloud = percent cloud cover, and wind = wind speed.

Species	Model	Negative Log-likelihood	k	AIC	ΔAIC	Weight	Cumulative Weight
ACFL	~date + time + noise + temp + clouds ~ 1	54.52	7	123.04	0.00	0.10	0.10
	~date + time + temp + clouds ~ 1	55.61	6	123.21	0.18	0.09	0.20
	~date + time + temp + clouds ~ 1	55.61	6	123.21	0.18	0.09	0.29
	~date + clouds ~ 1	57.75	4	123.51	0.47	0.08	0.37
	~date + time + clouds ~ 1	56.82	5	123.64	0.60	0.08	0.45
	~date + time + noise + clouds ~ 1	55.87	6	123.74	0.70	0.07	0.52
	~date + wind + clouds ~ 1	57.31	5	124.62	1.59	0.05	0.57
	~date + time + noise + temp + wind + clouds ~ 1	54.39	8	124.78	1.75	0.04	0.61
	~date + temp + clouds ~ 1	57.51	5	125.02	1.99	0.04	0.65
	~1 ~ 1	65.42	2	134.84	11.80	0.00	1.00
AMRO	~clouds ~ 1	56.80	3	119.60	0.00	0.06	0.06
	~date ~ 1	57.07	3	120.14	0.54	0.05	0.11
	~noise + clouds ~ 1	56.24	4	120.48	0.88	0.04	0.15
	~date + clouds ~ 1	56.28	4	120.55	0.95	0.04	0.19
	~1 ~ 1	58.28	2	120.57	0.96	0.04	0.22
	~date + wind ~ 1	56.33	4	120.65	1.05	0.04	0.26
	~temp ~ 1	57.33	3	120.67	1.07	0.04	0.30
	~wind ~ 1	57.39	3	120.78	1.18	0.03	0.33
	~wind + clouds ~ 1	56.50	4	121.00	1.40	0.03	0.36
	~temp + clouds ~ 1	56.62	4	121.24	1.64	0.03	0.39
	~date + temp ~ 1	56.66	4	121.33	1.73	0.03	0.41
	~temp + wind ~ 1	56.78	4	121.55	1.95	0.02	0.44

Continued

Table A.2. Continued

	~time + clouds ~ 1	56.79	4	121.59	1.99	0.02	0.46
	~date + time + noise + temp + wind + clouds ~ 1	55.45	8	126.91	7.30	0.00	1.00
	~date ~ 1	88.44	3	182.89	0.00	0.10	0.10
	~date + time ~ 1	88.07	4	184.13	1.24	0.05	0.15
	~date + wind ~ 1	88.22	4	184.44	1.55	0.05	0.20
	~date + noise ~ 1	88.26	4	184.51	1.62	0.04	0.24
	~date + clouds ~ 1	88.30	4	184.59	1.70	0.04	0.28
	~date + temp ~ 1	88.37	4	184.75	1.86	0.04	0.32
	~date + time + temp ~ 1	87.44	5	184.88	1.99	0.04	0.36
	~1 ~ 1	90.58	2	185.17	2.28	0.03	0.39
BGGN	~date ~ 1	88.44	3	182.89	0.00	0.10	0.10
	~date + time ~ 1	88.07	4	184.13	1.24	0.05	0.15
	~date + wind ~ 1	88.22	4	184.44	1.55	0.05	0.20
	~date + noise ~ 1	88.26	4	184.51	1.62	0.04	0.24
	~date + clouds ~ 1	88.30	4	184.59	1.70	0.04	0.28
	~date + temp ~ 1	88.37	4	184.75	1.86	0.04	0.32
	~date + time + temp ~ 1	87.44	5	184.88	1.99	0.04	0.36
	~1 ~ 1	90.58	2	185.17	2.28	0.03	0.39
	~date + time + noise + temp + wind + clouds ~ 1	86.04	8	188.09	5.20	0.01	0.91
CARW	~date ~ 1	66.33	3	138.66	0.00	0.07	0.07
	~date + clouds ~ 1	65.53	4	139.06	0.41	0.06	0.13
	~date + noise ~ 1	65.74	4	139.49	0.83	0.05	0.18
	~date + wind ~ 1	65.83	4	139.67	1.01	0.04	0.22
	~1 ~ 1	67.96	2	139.92	1.26	0.04	0.26
	~date + noise + clouds ~ 1	65.07	5	140.13	1.47	0.03	0.29
	~date + noise + wind ~ 1	65.08	5	140.17	1.51	0.03	0.32
	~date + time ~ 1	66.25	4	140.51	1.85	0.03	0.35
	~date + wind + clouds ~ 1	65.30	5	140.61	1.95	0.03	0.38
	~date + temp ~ 1	66.32	4	140.64	1.98	0.03	0.41
	~date + time + noise + temp + wind + clouds ~ 1	64.65	8	145.30	6.64	0.00	1.00
HOWR	~date + temp ~ 1	95.26	4	198.53	0.00	0.09	0.09
	~1 ~ 1	97.63	2	199.26	0.73	0.06	0.15

Continued

Table A.2. Continued

	~date ~ 1	96.71	3	199.41	0.88	0.06	0.20
	~time ~ 1	96.97	3	199.94	1.41	0.04	0.25
	~temp ~ 1	97.13	3	200.25	1.72	0.04	0.28
	~date + temp + clouds ~ 1	95.16	5	200.32	1.79	0.04	0.32
	~date + time ~ 1	96.18	4	200.36	1.83	0.03	0.35
	~date + temp + wind ~ 1	95.20	5	200.39	1.86	0.03	0.39
	~date + time + temp ~ 1	95.26	5	200.52	1.99	0.03	0.42
	~date + noise + temp ~ 1	95.26	5	200.52	1.99	0.03	0.45
	~date + time + noise + temp + wind + clouds ~ 1	95.11	8	206.22	7.69	0.00	1.00
INBU	~date + time + noise ~ 1	69.87	5	149.74	0.00	0.12	0.12
	~date + time ~ 1	70.94	4	149.87	0.13	0.11	0.22
	~date + time + wind ~ 1	70.65	5	151.30	1.56	0.05	0.28
	~date + time + noise + wind ~ 1	69.74	6	151.48	1.74	0.05	0.33
	~time + noise ~ 1	71.78	4	151.57	1.83	0.05	0.37
	~date + time + noise + clouds ~ 1	69.82	6	151.64	1.90	0.04	0.42
	~date + time + noise + temp ~ 1	69.85	6	151.70	1.96	0.04	0.46
	~date + time + clouds ~ 1	70.86	5	151.72	1.98	0.04	0.50
	~date + time + noise + temp + wind + clouds ~ 1	69.51	8	155.03	5.28	0.01	0.93
	~1 ~ 1	77.51	2	159.02	9.28	0.00	1.00
NOCA	~date ~ 1	88.89	3	183.79	0.00	0.11	0.11
	~date + noise ~ 1	88.05	4	184.10	0.32	0.09	0.20
	~date + noise + wind ~ 1	87.47	5	184.93	1.14	0.06	0.26
	~date + noise + temp ~ 1	87.49	5	184.98	1.19	0.06	0.32
	~date + temp ~ 1	88.64	4	185.28	1.49	0.05	0.37
	~date + wind ~ 1	88.66	4	185.33	1.54	0.05	0.42
	~date + time + noise ~ 1	87.80	5	185.59	1.81	0.04	0.46
	~date + time ~ 1	88.87	4	185.74	1.95	0.04	0.50
	~date + clouds ~ 1	88.89	4	185.78	1.99	0.04	0.54
	~1 ~ 1	92.45	2	188.89	5.11	0.01	0.89
	~date + time + noise + temp + wind + clouds ~ 1	86.79	8	189.58	5.80	0.01	0.94
NOPA	~1 ~ 1	65.67	2	135.33	0.00	0.09	0.09
	~date ~ 1	64.96	3	135.92	0.59	0.07	0.16

Continued

Table A.2. Continued

	~temp ~ 1	64.97	3	135.95	0.61	0.07	0.23
	~wind ~ 1	65.59	3	137.18	1.85	0.04	0.26
	~noise ~ 1	65.59	3	137.19	1.85	0.04	0.30
	~clouds ~ 1	65.61	3	137.23	1.89	0.04	0.33
	~time + temp ~ 1	64.62	4	137.25	1.92	0.04	0.37
	~time ~ 1	65.63	3	137.26	1.93	0.03	0.40
	~date + time + noise + temp + wind + clouds ~ 1	64.41	8	144.81	9.48	0.00	1.00
PARI	~wind ~ 1	96.59	3	199.18	0.00	0.09	0.09
	~clouds ~ 1	96.95	3	199.90	0.72	0.06	0.15
	~wind + clouds ~ 1	95.98	4	199.96	0.78	0.06	0.21
	~1 ~ 1	98.21	2	200.42	1.25	0.05	0.26
	~noise + wind ~ 1	96.34	4	200.68	1.50	0.04	0.30
	~time + wind ~ 1	96.49	4	200.97	1.80	0.04	0.34
	~date + wind ~ 1	96.49	4	200.99	1.81	0.04	0.37
	~temp + wind ~ 1	96.55	4	201.11	1.93	0.03	0.41
	~date + time + noise + temp + wind + clouds ~ 1	95.65	8	207.30	8.12	0.00	1.00
REVI	~1 ~ 1	70.87	2	145.73	0.00	0.08	0.08
	~temp ~ 1	70.28	3	146.57	0.83	0.06	0.14
	~time ~ 1	70.46	3	146.92	1.18	0.05	0.18
	~clouds ~ 1	70.56	3	147.12	1.38	0.04	0.23
	~noise ~ 1	70.56	3	147.12	1.39	0.04	0.27
	~wind ~ 1	70.72	3	147.44	1.70	0.04	0.30
	~noise + temp ~ 1	69.72	4	147.44	1.70	0.04	0.34
	~time + noise ~ 1	69.77	4	147.53	1.80	0.03	0.37
	~date ~ 1	70.87	3	147.73	2.00	0.03	0.40
	~date + time + noise + temp + wind + clouds ~ 1	68.97	8	153.95	8.21	0.00	1.00
ALL	~date + temp ~ 1	205.76	4	419.52	0.00	0.09	0.09
	~date + time + temp ~ 1	205.01	5	420.02	0.51	0.07	0.16
	~date + temp + clouds ~ 1	205.32	5	420.64	1.13	0.05	0.21
	~time ~ 1	207.34	3	420.69	1.17	0.05	0.25
	~date + time + temp + wind ~ 1	204.35	6	420.70	1.18	0.05	0.30
	~date + temp + wind ~ 1	205.45	5	420.90	1.38	0.04	0.35

Continued

Table A.2. Continued

	~time + wind ~ 1	206.53	4	421.06	1.55	0.04	0.39
	~date + noise + temp ~ 1	205.56	5	421.12	1.61	0.04	0.43
	~time + temp ~ 1	206.61	4	421.23	1.71	0.04	0.46
	~date + time + noise + temp + wind + clouds ~ 1	204.18	8	424.36	4.84	0.01	0.93
	~1 ~ 1	211.63	2	427.26	7.74	0.00	0.99
LD	~date + temp ~ 1	153.47	4	314.93	0.00	0.15	0.15
	~date + temp + wind ~ 1	152.77	5	315.54	0.61	0.11	0.26
	~date + temp + clouds ~ 1	153.24	5	316.48	1.55	0.07	0.33
	~date + temp + wind + clouds ~ 1	152.31	6	316.63	1.70	0.06	0.40
	~date + noise + temp ~ 1	153.44	5	316.88	1.95	0.06	0.45
	~date + time + temp ~ 1	153.47	5	316.93	2.00	0.06	0.51
	~date + time + noise + temp + wind + clouds ~ 1	152.16	8	320.32	5.39	0.01	0.84
	~1 ~ 1	158.91	2	321.82	6.89	0.00	0.92
SD	~clouds ~ 1	164.89	3	335.79	0.00	0.10	0.10
	~temp + clouds ~ 1	164.49	4	336.99	1.20	0.06	0.16
	~time + clouds ~ 1	164.51	4	337.02	1.24	0.06	0.21
	~1 ~ 1	166.66	2	337.32	1.53	0.05	0.26
	~date + clouds ~ 1	164.76	4	337.52	1.73	0.04	0.31
	~noise + clouds ~ 1	164.89	4	337.78	1.99	0.04	0.34
	~wind + clouds ~ 1	164.89	4	337.79	2.00	0.04	0.38
	~date + time + noise + temp + wind + clouds ~ 1	164.03	8	344.06	8.28	0.00	1.00
OW	~date + time ~ 1	164.98	4	337.96	0.00	0.10	0.10
	~date + temp ~ 1	165.16	4	338.32	0.36	0.08	0.18
	~date + time + wind ~ 1	164.18	5	338.37	0.40	0.08	0.27
	~date + time + temp ~ 1	164.24	5	338.47	0.51	0.08	0.34
	~date + time + temp + wind ~ 1	163.47	6	338.94	0.98	0.06	0.41
	~date + time + noise ~ 1	164.60	5	339.20	1.24	0.05	0.46
	~date + time + wind + clouds ~ 1	163.84	6	339.69	1.72	0.04	0.50
	~date + temp + wind ~ 1	164.84	5	339.69	1.72	0.04	0.55
	~date + time + noise + temp ~ 1	163.89	6	339.79	1.82	0.04	0.59
	~date + time + clouds ~ 1	164.89	5	339.79	1.83	0.04	0.63
	~date + time + noise + wind ~ 1	163.93	6	339.86	1.90	0.04	0.67

Continued

Table A.2. Continued

	~date + time + noise + temp + wind + clouds ~ 1	163.19	8	342.38	4.41	0.01	0.97
	~1 ~ 1	174.91	2	353.82	15.85	0.00	1.00
WOOD	~time + wind ~ 1	97.86	4	203.71	0.00	0.07	0.07
	~1 ~ 1	100.04	2	204.09	0.38	0.06	0.14
	~time ~ 1	99.08	3	204.15	0.44	0.06	0.20
	~wind ~ 1	99.40	3	204.80	1.09	0.04	0.24
	~date + time + wind ~ 1	97.64	5	205.28	1.56	0.03	0.27
	~noise ~ 1	99.67	3	205.33	1.62	0.03	0.31
	~time + noise + wind ~ 1	97.67	5	205.35	1.63	0.03	0.34
	~noise + wind ~ 1	98.83	4	205.65	1.94	0.03	0.37
	~temp ~ 1	99.83	3	205.66	1.95	0.03	0.40
	~time + temp + wind ~ 1	97.86	5	205.71	2.00	0.03	0.42
	~time + wind + clouds ~ 1	97.86	5	205.71	2.00	0.03	0.45
	~date + time + noise + temp + wind + clouds ~ 1	97.41	8	210.82	7.11	0.00	1.00
SN	~date + time + noise ~ 1	120.83	5	251.67	0.00	0.18	0.18
	~date + time ~ 1	122.23	4	252.46	0.79	0.12	0.30
	~date + time + noise + wind ~ 1	120.79	6	253.57	1.90	0.07	0.37
	~date + time + noise + clouds ~ 1	120.81	6	253.62	1.96	0.07	0.44
	~date + time + noise + temp ~ 1	120.83	6	253.67	2.00	0.07	0.51
	~date + time + noise + temp + wind + clouds ~ 1	120.73	8	257.45	5.78	0.01	0.89
	~1 ~ 1	131.03	2	266.07	14.40	0.00	1.00

Table A.3. N-mixture model AIC table for the abundance models with a ΔAIC greater than 2 and less than 7. Null and global models with a ΔAIC greater than 7 are also included; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Coefficients for removed honeysuckle status are listed when applicable. Asterisks are next to removed plot estimates when the estimates of honeysuckle status have significance and next to model names when variables other than honeysuckle status are significant. "*" designates a weak effect if any ($P < 0.15$), "**" represents a moderate effect ($P < 0.10$), "***" designates a strong effect ($P < 0.05$). American Ornithological Society alpha banding codes designate the avian species (exception: PARI = CACH and TUTI). ALL = all species combined, LD = medium-long distance migrants, SD = resident-medium distance migrants, OW = species preferring open woodland habitat, WOOD = woodpeckers, and SN = shrub nesters.

Species	Model	Removed plot estimate (±SE)	Negative log-likelihood	k	AIC	ΔAIC	Weight	Cumulative weight
ACFL	Basal area	1 (±0.63)*	52.30	9	122.61	2.38	0.09	0.64
	Null	n/a	54.52	7	123.04	2.80	0.07	0.71
	Canopy cover	1.06 (±0.62)**	52.63	9	123.27	3.04	0.06	0.77
	Plot-bordering honeysuckle	1.03 (±0.68)*	52.71	9	123.41	3.18	0.06	0.83
	Deadwood	1.05 (±0.63)**	52.71	9	123.42	3.19	0.06	0.88
	Canopy composition	1.06 (±0.63)**	52.71	9	123.43	3.19	0.06	0.94
	Reduced canopy	n/a	52.87	9	123.73	3.50	0.05	0.99
	Canopy*	n/a	52.57	11	127.14	6.91	0.01	1.00
	Global	0.69 (±0.72)	51.38	14	130.75	10.52	0.00	1.00
AMRO	Null	n/a	56.80	3	119.60	3.22	0.06	0.77
	Canopy crown length**	0.29 (±0.52)	55.05	5	120.10	3.72	0.05	0.82
	Canopy cover**	0.09 (±0.52)	55.21	5	120.42	4.04	0.04	0.86

Continued

Table A.3. Continued

	Global*	0.19 (±0.63)	50.51	10	121.02	4.65	0.03	0.90
	Canopy composition	0.13 (±0.52)	55.70	5	121.40	5.02	0.03	0.92
	Honeysuckle status	0.15 (±0.52)	56.76	4	121.52	5.14	0.02	0.95
	Honeysuckle cover	n/a	56.80	4	121.60	5.22	0.02	0.97
	Plot-bordering honeysuckle	-0.21 (±0.6)	56.01	5	122.03	5.65	0.02	0.99
BGGN	Canopy composition	0.19 (±0.34)	87.65	5	185.30	2.41	0.09	0.66
	Canopy crown length	0.19 (±0.35)	87.99	5	185.99	3.10	0.06	0.72
	Canopy cover	0.23 (±0.34)	88.10	5	186.20	3.31	0.06	0.77
	Plot-bordering honeysuckle	0.3 (±0.38)	88.13	5	186.26	3.37	0.05	0.83
	Reduced canopy	n/a	88.15	5	186.31	3.42	0.05	0.88
	Deadwood	0.21 (±0.35)	88.16	5	186.32	3.43	0.05	0.93
	Basal area	0.23 (±0.34)	88.20	5	186.40	3.51	0.05	0.98
	Canopy	n/a	87.17	7	188.35	5.46	0.02	1.00
	Global	0.22 (±0.4)	86.92	10	193.84	10.95	0.00	1.00
CARW	Canopy cover	0.12 (±0.38)	65.78	5	141.55	2.90	0.06	0.80
	Deadwood	0.17 (±0.38)	66.07	5	142.14	3.49	0.05	0.85
	Plot-bordering honeysuckle	0.03 (±0.43)	66.17	5	142.33	3.68	0.04	0.89
	Canopy composition	0.14 (±0.38)	66.23	5	142.47	3.81	0.04	0.93

Continued

Table A.3. Continued

	Basal area	0.13 (±0.38)	66.27	5	142.54	3.88	0.04	0.97
	Canopy*	n/a	64.71	7	143.43	4.77	0.02	1.00
	Global	0.04 (±0.46)	64.56	10	149.12	10.46	0.00	1.00
HOWR	Canopy composition	0.46 (±0.35)	93.53	6	199.05	2.04	0.09	0.76
	Deadwood	0.55 (±0.35)*	93.80	6	199.60	2.58	0.07	0.82
	Canopy cover	0.49 (±0.35)	93.96	6	199.93	2.91	0.06	0.88
	Reduced canopy*	n/a	94.13	6	200.27	3.25	0.05	0.93
	Basal area	0.5 (±0.35)	94.15	6	200.29	3.27	0.05	0.98
	Canopy*	n/a	93.12	8	202.23	5.22	0.02	1.00
	Global	0.16 (±0.4)	91.41	11	204.83	7.81	0.00	1.00
INBU	Canopy composition	0.48 (±0.38)	68.81	7	151.63	2.07	0.07	0.73
	Plot-bordering honeysuckle	0.43 (±0.42)	68.92	7	151.83	2.28	0.06	0.79
	Basal area	0.5 (±0.38)	68.93	7	151.85	2.29	0.06	0.84
	Canopy crown length	0.48 (±0.39)	68.96	7	151.93	2.37	0.06	0.90
	Deadwood	0.49 (±0.39)	68.97	7	151.93	2.38	0.06	0.96
	Reduced canopy	n/a	69.77	7	153.55	3.99	0.03	0.98
	Canopy	n/a	68.35	9	154.69	5.14	0.01	1.00
	Global	0.39 (±0.45)	67.60	12	159.20	9.65	0.00	1.00
NOCA	Basal area	-0.23 (±0.28)	88.02	5	186.04	2.25	0.08	0.71

Continued

Table A.3. Continued

	Deadwood	-0.21 (±0.29)	88.32	5	186.65	2.86	0.06	0.77
	Reduced canopy	n/a	88.33	5	186.66	2.87	0.06	0.83
	Canopy cover	-0.24 (±0.29)	88.43	5	186.86	3.08	0.05	0.88
	Plot-bordering honeysuckle	-0.3 (±0.34)	88.49	5	186.98	3.20	0.05	0.93
	Canopy crown length	-0.24 (±0.29)	88.52	5	187.04	3.25	0.05	0.98
	Canopy	n/a	87.41	7	188.81	5.02	0.02	1.00
	Global	-0.09 (±0.32)	85.83	10	191.66	7.87	0.00	1.00
NOPA	Honeysuckle cover	n/a	64.69	4	137.38	2.75	0.07	0.72
	Honeysuckle status	0.25 (±0.39)	64.75	4	137.49	2.86	0.07	0.78
	Canopy cover	0.24 (±0.39)	64.16	5	138.32	3.68	0.04	0.82
	Canopy**	n/a	62.24	7	138.49	3.86	0.04	0.86
	Deadwood	0.19 (±0.39)	64.29	5	138.57	3.94	0.04	0.90
	Canopy crown length	0.32 (±0.4)	64.37	5	138.74	4.10	0.04	0.94
	Canopy composition	0.22 (±0.39)	64.55	5	139.09	4.46	0.03	0.97
	Plot-bordering honeysuckle	0.13 (±0.44)	64.56	5	139.13	4.50	0.03	1.00
	Global	0.13 (±0.47)	61.86	10	143.72	9.09	0.00	1.00
PARI	Plot-bordering honeysuckle	-0.16 (±0.32)	95.93	5	201.87	2.69	0.07	0.71
	Basal area	-0.25 (±0.29)	96.04	5	202.08	2.90	0.06	0.77
	Canopy crown length	-0.24 (±0.29)	96.08	5	202.15	2.97	0.06	0.82

Continued

Table A.3. Continued

	Deadwood	-0.25 (±0.29)	96.09	5	202.17	3.00	0.06	0.88
	Canopy cover	-0.27 (±0.29)	96.16	5	202.32	3.14	0.05	0.94
	Reduced canopy	n/a	96.31	5	202.61	3.43	0.05	0.98
	Canopy	n/a	95.32	7	204.63	5.45	0.02	1.00
	Global	0.1 (±0.37)	94.54	10	209.08	9.90	0.00	1.00
REVI	Honeysuckle cover	n/a	70.25	4	148.50	2.06	0.07	0.82
	Canopy cover	-0.39 (±0.4)	69.38	5	148.76	2.31	0.06	0.88
	Canopy	n/a	67.76	7	149.52	3.07	0.04	0.92
	Plot-bordering honeysuckle	-0.41 (±0.46)	69.85	5	149.70	3.25	0.04	0.96
	Deadwood	-0.36 (±0.4)	69.85	5	149.71	3.26	0.04	0.99
	Global	-0.74 (±0.52)	66.74	10	153.49	7.04	0.01	1.00
SN	Canopy cover*	0.12 (±0.13)	163.48	5	336.96	2.43	0.07	0.70
	Honeysuckle status	0.12 (±0.14)	164.49	4	336.97	2.44	0.07	0.77
	Honeysuckle cover	n/a	164.77	4	337.54	3.01	0.05	0.82
	Deadwood	0.16 (±0.14)	163.79	5	337.57	3.05	0.05	0.87
	Canopy**	n/a	161.99	7	337.98	3.46	0.04	0.92
	Canopy composition	0.11 (±0.14)	164.08	5	338.15	3.62	0.04	0.96
	Canopy crown length	0.12 (±0.14)	164.48	5	338.97	4.44	0.03	0.98
	Global**	0.13 (±0.15)	159.79	10	339.58	5.06	0.02	1.00

Continued

Table A.3. Continued

LD	Plot-bordering honeysuckle	0.05 (±0.16)	152.72	6	317.45	2.52	0.08	0.61
	Basal area	0.12 (±0.14)	152.74	6	317.49	2.55	0.08	0.69
	Canopy composition	0.1 (±0.14)	152.85	6	317.71	2.77	0.07	0.76
	Canopy cover	0.11 (±0.14)	152.90	6	317.80	2.87	0.06	0.82
	Canopy crown length	0.13 (±0.14)	152.95	6	317.90	2.97	0.06	0.88
	Reduced canopy	n/a	153.07	6	318.13	3.20	0.05	0.94
	Deadwood	0.12 (±0.14)	153.10	6	318.19	3.26	0.05	0.99
	Canopy	n/a	152.70	8	321.40	6.47	0.01	1.00
	Global		151.86	11	325.72	10.78	0.00	1.00
SN	Plot-bordering honeysuckle	-0.17 (±0.21)	119.85	7	253.71	2.04	0.08	0.73
	Reduced canopy	n/a	120.10	7	254.20	2.53	0.06	0.79
	Basal area	-0.01 (±0.18)	120.15	7	254.30	2.63	0.06	0.85
	Canopy cover	-0.03 (±0.18)	120.27	7	254.53	2.86	0.05	0.91
	Canopy*	n/a	118.40	9	254.81	3.14	0.05	0.95
	Canopy crown length	0 (±0.19)	120.70	7	255.40	3.74	0.03	0.99
	Global	-0.04 (±0.22)	116.63	12	257.27	5.60	0.01	1.00
OW	Canopy composition***	0.25 (±0.14)**	160.64	6	333.27	2.34	0.11	0.79
	Basal area***	0.29 (±0.14)***	161.08	6	334.16	3.23	0.07	0.86
	Canopy***	n/a	159.23	8	334.45	3.52	0.06	0.92
	Honeysuckle status	0.28 (±0.15)**	163.13	5	336.25	5.32	0.02	0.94

Continued

Table A.3. Continued

	Deadwood	0.31 (±0.15)***	162.29	6	336.59	5.66	0.02	0.96
	Honeysuckle cover	n/a	163.94	5	337.87	6.94	0.01	0.97
	Null		164.98	4	337.96	7.03	0.01	0.98
WOOD	Honeysuckle status	0.79 (±0.33)***	94.59	5	199.17	2.25	0.12	0.66
	Canopy composition	0.82 (±0.34)***	93.82	6	199.63	2.71	0.10	0.75
	Basal area	0.77 (±0.34)***	94.35	6	200.70	3.78	0.06	0.81
	Canopy cover	0.78 (±0.33)***	94.37	6	200.74	3.82	0.06	0.87
	Deadwood	0.81 (±0.34)***	94.47	6	200.93	4.01	0.05	0.92
	Canopy crown length	0.8 (±0.34)***	94.54	6	201.07	4.15	0.05	0.97
	Global***	1.32 (±0.41)***	90.65	11	203.29	6.37	0.02	0.98
	Null	n/a	97.86	4	203.71	6.79	0.01	1.00
ALL	Deadwood	0.16 (±0.09)**	208.39	6	428.77	2.16	0.08	0.68
	Null	n/a	210.39	4	428.78	2.16	0.08	0.76
	Honeysuckle cover	n/a	209.56	5	429.12	2.51	0.07	0.83
	Reduced canopy**	n/a	208.86	6	429.73	3.11	0.05	0.88
	Canopy crown length	0.16 (±0.09)**	208.89	6	429.78	3.17	0.05	0.93
	Canopy composition	0.15 (±0.09)*	209.00	6	430.00	3.39	0.04	0.98
	Global	0.15 (±0.1)	205.16	11	432.31	5.70	0.01	0.99
	Canopy	n/a	208.52	8	433.04	6.43	0.01	1.00

Table A.4. Diversity and richness GLM AICc tables for models with a ΔAIC greater than 2 and less than 7; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Null and global models with a ΔAIC greater than 7 are also included. Coefficients for removed honeysuckle status are listed when applicable. Asterisks are next to removed plot estimates when the estimates of honeysuckle status have significance and next to model names when variables other than honeysuckle status are significant. "*" designates a weak effect if any ($P < 0.15$), "**" represents a moderate effect ($P < 0.10$), "***" designates a strong effect ($P < 0.05$).

	Model names	Removed plot estimate (±SE)	K	AICc	ΔAICc	AICc Weight	Log-likelihood	Cumulative weight	R^2
Diversity	Plot-bordering honeysuckle	0.06 (±0.09)	4	-7.56	2.20	0.08	8.73	0.72	0.13
	Honeysuckle cover	n/a	3	-7.47	2.28	0.07	7.28	0.80	0.03
	Canopy cover	0.11 (±0.08)	4	-7.18	2.57	0.06	8.54	0.86	0.12
	Reduced canopy	n/a	4	-6.99	2.76	0.06	8.45	0.92	0.11
	Deadwood	0.12 (±0.08)*	4	-6.37	3.38	0.04	8.14	0.96	0.09
	Canopy composition	0.11 (±0.08)	4	-6.03	3.73	0.04	7.97	1.00	0.08
	Global	0.12 (±0.09)	9	3.91	13.66	0.00	12.67	1.00	0.36
Richness	Reduced canopy	n/a	4	142.52	2.56	0.05	-66.31	0.92	0.10
	Deadwood	2.16 (±1.43)*	4	142.88	2.93	0.04	-66.49	0.96	0.09
	Canopy composition	2.09 (±1.42)	4	142.91	2.95	0.04	-66.50	1.00	0.09
	Global	1.86 (±1.68)	9	154.06	14.10	0.00	-62.40	1.00	0.34

Table A.5. Coefficient estimates (other than the removed plot estimate) of all top (AICc < 2) avian diversity and richness GLMs as well as top (AIC < 2) abundance functions for all N-mixture models; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Estimates are not back-transformed. "*" designates a weak effect if any (*P* < 0.15), "**" represents a moderate effect (*P* < 0.10), "***" designates a strong effect (*P* < 0.05). American Ornithological Society alpha banding codes designate the avian species (exception: PARI = CACH and TUTI). ALL = all species combined, LD = medium-long distance migrants, SD = resident-medium distance migrants, OW = species preferring open woodland habitat, WOOD = woodpeckers, and SN = shrub nesters.

Species	Model	Basal area (±SE)	Canopy cover (±SE)	Canopy crown length (±SE)	Dead wood (±SE)	Honey-suckle cover (±SE)	Intercept (±SE)	Plot-bordering honeysuckle (±SE)	Canopy composition (±SE)
ACFL	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.6 (±0.32)**	0.79 (±1.24)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	-0.1 (±0.88)	n/a	n/a
	Canopy crown length	n/a	n/a	0.24 (±0.21)	n/a	n/a	-0.02 (±0.9)	n/a	n/a
AMRO	Canopy	-0.36 (±0.28)	-0.43 (±0.24)**	-0.5 (±0.29)**	n/a	n/a	-0.11 (±0.47)	n/a	-0.23 (±0.25)
	Reduced canopy	-0.47 (±0.27)**	n/a	-0.28 (±0.25)	n/a	n/a	-0.06 (±0.37)	n/a	n/a
	Basal area	-0.59 (±0.27)***	n/a	n/a	n/a	n/a	-0.15 (±0.52)	n/a	n/a
BGGN	Null	n/a	n/a	n/a	n/a	n/a	0.83 (±0.29)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.13 (±0.16)	0.83 (±0.3)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	0.67 (±0.39)	n/a	n/a
CARW	Null	n/a	n/a	n/a	n/a	n/a	3.2 (±8.26)	n/a	n/a
	Reduced canopy	-0.07 (±0.19)	n/a	0.28 (±0.17)*	n/a	n/a	3.79 (±0.84)	n/a	n/a
	Canopy crown length	n/a	n/a	0.26 (±0.17)*	n/a	n/a	3.78 (±0.86)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.08 (±0.18)	4.09 (±3.79)	n/a	n/a

Continued

Table A.5. Continued

	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	3.36 (±10.56)	n/a	n/a

Table A.4. Continued

HOWR	Plot-bordering honeysuckle	n/a	n/a	n/a	n/a	n/a	0.95 (±0.45)	-0.29 (±0.16)**	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	0.7 (±0.41)	n/a	n/a
	Null	n/a	n/a	n/a	n/a	n/a	1.01 (±0.29)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.2 (±0.16)	1.04 (±0.32)	n/a	n/a
	Canopy crown length	n/a	n/a	0.17 (±0.15)	n/a	n/a	0.76 (±0.43)	n/a	n/a
INBU	Canopy cover	n/a	-0.22 (±0.14)*	n/a	n/a	n/a	3.46 (±0.77)	n/a	n/a
	Null	n/a	n/a	n/a	n/a	n/a	4.21 (±1.21)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	3.75 (±1)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.23 (±0.18)	4.09 (±0.91)	n/a	n/a
NOCA	Null	n/a	n/a	n/a	n/a	n/a	1.58 (±0.97)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	0.14 (±0.13)	1.62 (±1.03)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	1.76 (±0.98)	n/a	n/a
	Canopy composition	n/a	n/a	n/a	n/a	n/a	2.25 (±1.96)	n/a	-0.18 (±0.14)
NOPA	Basal area	-0.39 (±0.18)***	n/a	n/a	n/a	n/a	3.47 (±0.71)	n/a	n/a
	Reduced canopy	-0.4 (±0.2)***	n/a	-0.01 (±0.18)	n/a	n/a	3.68 (±0.67)	n/a	n/a
	Null	n/a	n/a	n/a	n/a	n/a	4.23 (±0.82)	n/a	n/a
PARI	Null	n/a	n/a	n/a	n/a	n/a	1.68 (±0.66)	n/a	n/a

Continued

Table A.5. Continued

	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	1.79 (±0.61)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	0.12 (±0.13)	1.61 (±0.62)	n/a	n/a
	Canopy composition	n/a	n/a	n/a	n/a	n/a	1.86 (±0.7)	n/a	0.15 (±0.13)
REVI	Basal area	0.35 (±0.19)**	n/a	n/a	n/a	n/a	1.01 (±0.63)	n/a	n/a
	Null	n/a	n/a	n/a	n/a	n/a	0.65 (±0.49)	n/a	n/a
	Reduced canopy	0.32 (±0.2)*	n/a	0.17 (±0.21)	n/a	n/a	0.53 (±0.47)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	0.93 (±0.58)	n/a	n/a
	Canopy crown length	n/a	n/a	0.27 (±0.21)	n/a	n/a	0.86 (±0.51)	n/a	n/a
	Canopy composition	n/a	n/a	n/a	n/a	n/a	0.85 (±0.6)	n/a	0.22 (±0.18)
SD	Basal area	-0.13 (±0.06)***	n/a	n/a	n/a	n/a	3.52 (±1.23)	n/a	n/a
	Reduced canopy	-0.14 (±0.07)***	n/a	0.05 (±0.06)	n/a	n/a	3.49 (±1.11)	n/a	n/a
	Null	n/a	n/a	n/a	n/a	n/a	3.13 (±0.67)	n/a	n/a
	Plot-bordering honeysuckle	n/a	n/a	n/a	n/a	n/a	3.44 (±1.01)	-0.11 (±0.07)*	n/a
LD	Null	n/a	n/a	n/a	n/a	n/a	3.05 (±1.1)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	3.07 (±1.33)	n/a	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.05 (±0.07)	3.11 (±1.22)	n/a	n/a
SN	Null	n/a	n/a	n/a	n/a	n/a	3.2 (±2.23)	n/a	n/a
	Canopy composition	n/a	n/a	n/a	n/a	n/a	4.09 (±0.61)	n/a	-0.17 (±0.09)**

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Table A.5. Continued

	Honeysuckle cover	n/a	n/a	n/a	n/a	0.03 (±0.09)	3.31 (±2.53)	n/a	n/a
	Deadwood	n/a	n/a	n/a	0.13 (±0.09)	n/a	4.13 (±0.78)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	3.26 (±2.36)	n/a	n/a
OW	Global	-0.07 (±0.07)	-0.1 (±0.06)*	-0.04 (±0.07)	0.08 (±0.06)	n/a	3.82 (±0.3)	-0.11 (±0.07)*	-0.12 (±0.07)**
	Plot-bordering honeysuckle	n/a	n/a	n/a	n/a	n/a	3.38 (±0.95)	-0.18 (±0.07)***	n/a
	Canopy cover	n/a	-0.15 (±0.06)***	n/a	n/a	n/a	3.28 (±1.03)	n/a	n/a
WOOD	Plot-bordering honeysuckle	n/a	n/a	n/a	n/a	n/a	3.06 (±0.52)	0.28 (±0.14)***	n/a
	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.39 (±0.16)***	4.05 (±0.39)	n/a	n/a
ALL	Basal area	-0.07 (±0.04)**	n/a	n/a	n/a	n/a	4.06 (±0.63)	n/a	n/a
	Plot-bordering honeysuckle	n/a	n/a	n/a	n/a	n/a	4.07 (±0.58)	-0.07 (±0.04)*	n/a
Richness	Null	n/a	n/a	n/a	n/a	n/a	16.46 (±0.65)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	15 (±1.15)	n/a	n/a
	Canopy crown length	n/a	n/a	-0.99 (±0.65)*	n/a	n/a	14.7 (±1.14)	n/a	n/a
	Basal area	-0.96 (±0.63)*	n/a	n/a	n/a	n/a	14.91 (±1.12)	n/a	n/a
	Plot-bordering hs	n/a	n/a	n/a	n/a	n/a	15.7 (±1.23)	-1.02 (±0.73)	n/a
	Canopy cover	n/a	-0.71 (±0.65)	n/a	n/a	n/a	15 (±1.14)	n/a	n/a

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Table A.5. Continued

	Honeysuckle cover	n/a	n/a	n/a	n/a	-0.62 (±0.67)	16.46 (±0.66)	n/a	n/a
Diversity	Canopy crown length	n/a	n/a	-0.07 (±0.04)*	n/a	n/a	2.52 (±0.06)	n/a	n/a
	Null	n/a	n/a	n/a	n/a	n/a	2.62 (±0.04)	n/a	n/a
	Honeysuckle status	n/a	n/a	n/a	n/a	n/a	2.54 (±0.07)	n/a	n/a
	Basal area	-0.05 (±0.04)	n/a	n/a	n/a	n/a	2.53 (±0.06)	n/a	n/a

Table A.6. Model-averaged predicted abundances and detection probabilities from N-mixture models as well species richness and diversity model-averaged predictions from GLMs; data collected in Greene County, OH along the Little Miami River during the 2019 peak breeding season. Where "i" represents plots invaded by honeysuckle, and "r" represent plots removed of honeysuckle. Lower and Upper = 95% confidence intervals around predicted values. ALL = all species combined, LD = medium-long distance migrants, SD = resident-medium distance migrants, OW = species preferring open woodland habitat, WOOD = woodpeckers, and SN = shrub-nesters. American Ornithological Society alpha banding codes designate the avian species (exceptions: PARI = CACH and TUTI). i = invaded plots and r = removed plots.

Species	Honeysuckle Status	Predicted Abundance	Lower	Upper	Predicted Detection Probability	Lower	Upper
ACFL	i	0.94 (±0.83)	0.16	5.32	0.13 (±0.13)	0.02	0.60
	r	2.53 (±1.89)	0.58	10.97			
AMRO	i	0.9 (±0.4)	0.38	2.17	0.35 (±0.14)	0.14	0.65
	r	0.92 (±0.39)	0.41	2.10			
BGGN	i	2.18 (±0.71)	1.17	4.09	0.44 (±0.13)	0.22	0.68
	r	2.35 (±0.71)	1.30	4.24			
CARW	i	30.69 (±131.22)	3.01	193817249.00	0.01 (±0.09)	0.00	0.68
	r	31.39 (±136.26)	3.16	213678381.00			
HOWR	i	2.41 (±1.02)	1.10	5.36	0.35 (±0.12)	0.17	0.60
	r	3.1 (±1.11)	1.56	6.17			
INBU	i	46.4 (±57.74)	5.39	583.04	0.01 (±0.01)	0.00	0.07
	r	61.15 (±66.63)	9.15	639.25			
NOCA	i	6.15 (±8.22)	0.65	124.25	0.16 (±0.18)	0.02	0.73
	r	5.3 (±6.84)	0.58	102.40			
NOPA	i	42.87 (±33.88)	10.22	182.50	0.01 (±0.01)	0.00	0.04
	r	46.51 (±33.99)	12.02	185.05			
PARI	i	5.74 (±3.78)	1.60	20.72	0.17 (±0.11)	0.04	0.49
	r	5.1 (±3.42)	1.38	18.90			
REVI	i	2.24 (±1.32)	0.76	6.75	0.26 (±0.13)	0.09	0.58
	r	1.74 (±0.91)	0.63	4.82			
ALL	i	57.85 (±36.27)	16.95	197.83	0.19 (±0.12)	0.05	0.51
	r	65.56 (±41.5)	19.01	226.53			
SD	i	30.92 (±33.86)	4.03	272.80	0.15 (±0.16)	0.02	0.66

Continued

Table A.6. Continued

	r	32.91 (±36.77)	4.17	298.42			
LD	i	20.15 (±22.91)	2.27	196.15	0.22 (±0.25)	0.02	0.83
	r	21 (±24.05)	2.33	206.80			
SN	i	41.12 (±51.84)	8.32	1345.95	0.06 (±0.12)	0.00	0.59
	r	37.15 (±22.43)	8.01	1328.91			
OW	i	37.15 (±22.43)	15.08	136.37	0.11 (±0.08)	0.03	0.36
	r	43.98 (±25.94)	18.68	157.70			
WOOD	i	21.29 (±11.15)	7.63	59.40	0.02 (±0.01)	0.01	0.04
	r	60.06 (±20.89)	30.37	118.75			
Richness	i	15.45 (±1.25)	12.99	17.90	n/a	n/a	
	r	16.91 (±0.8)	15.35	18.47			
Diversity	i	2.55 (±0.07)	2.41	2.69	n/a	n/a	
	r	2.65 (±0.05)	2.56	2.73			