The Effects of Human Activity on Avian Communities in the Baraboo Hills

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at the University of Wisconsin-Madison

Abstract

While the intent of establishing protected areas was originally to preserve natural areas for human enjoyment, most have now taken on the role of both providing recreational opportunities such as hiking, and protecting habitats, flora, and fauna. While many protected areas prohibit development within their boundaries, they attract development around their periphery. Such development increases conservation pressure on the associated protected area by changing land use patterns outside the protected area, and inside the protected area with potentially increased recreational use. Understanding whether these anthropogenic changes in and near protected areas have demographic, community, or distributional consequences for native species is vital to our ability to maintain species diversity and densities that ensure population persistence. Within the context of this broader question, I examined whether the rural development around protected areas and recreational trails and trail use within protected areas have altered bird communities in a 22,000 ha forested region of southern WI, the Baraboo Hills.

Forest songbirds are threatened by the construction of houses within forests and associated loss of forest land cover. In parallel with many forested regions of North America, the Baraboo Hills residential development has increased in recent decades. I investigated whether forest bird communities have changed in the Baraboo Hills using bird surveys within protected areas from the late 1970s and repeat surveys conducted in the early 2000s. I found that overall there was no change in forest cover or housing density between survey periods within the extent of our study area. Bird communities have become more similar between surveys. This change in community structure was not associated with forest cover change or housing density, but appears to have been primarily associated with successional changes of the forest, with 1970s early successional forests becoming more mature. This resulted in the loss of species associated with early successional forests (e.g. Eastern Towhee (*Pipilo erythrophthalmus*), Gray Catbird (*Dumetella carolinensis*), and Golden-winged Warbler (*Vermivora chrysoptera*)) and gain of interior forest species (e.g. Red-eyed Vireo (*Vireo olivaceus*) and Ovenbird (*Seiurus aurocapilla*)). It appears that local conservation efforts have maintained, and promoted, forest species in the area.

Trails in forested protected areas facilitate the penetration of human disturbance into otherwise contiguous forests. Such disturbance may alter bird communities by excluding species sensitive to human presence and disturbance, while the physical attributes of recreational trails used for access may fragment otherwise contiguous forests, and facilitate development of vegetation characteristics typically associated with edges, such as increased foliage volume. I found that while bird species richness was not associated with recreational trails or trail use, the densities of most species were negatively associated with both trail use and trail width.

Trails and trail use can also affect nest success, possibly by altering nest attendance behavior. I found that the nest success of Acadian Flycatchers (*Empidonax virescens*) was negatively associated with trail use. This suggests that both the presence of humans, and the presence of the trail itself, negatively affect forest bird communities. I recommend that the construction of new trails in forested protected areas should be limited, and that trail width should be minimized for newly constructed trails. Very wide trails (>2 m) should be remediated with natural vegetation to reduce trail width.

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Introduction

Human land use and activities can have unintended negative consequences for natural communities and wildlife habitat. Protected areas, important for the preservation of biodiversity, are threatened by anthropogenic actions, such as land-cover change including housing density growth (Radeloff et al. 2010; Wade et al. 2011; Wood et al. 2015) and non-consumptive land use activities including recreation (Boyle & Samson 1985; Steven et al. 2011). These anthropogenic changes near and in protected areas degrade their ecological integrity, and as a result protected areas are expected to lose 5-12% of their effective area by mid-century (Wade & Theobald 2010; Martinuzzi et al. 2013). A number of conditions and processes that erode ecological integrity are attributable to low housing density in rural areas (e.g. increased exotic species (Gavier-Pizarro et al. 2010), and simplification of native plant communities (Odell & Knight 2001)). Rural development is associated with both forest fragmentation and loss, while associated infrastructure, such as roads and powerlines, further increase forest fragmentation (Forman & Alexander 1998; Parendes & Jones 2000; Hawbaker et al. 2006).

Not only are plants and forest structure affected by low density housing, but birds too may suffer erosion of habitat quality in areas of low housing density. As housing density increases from undeveloped areas to the urban core, bird species richness increases, peaking in the middle of the housing density gradient, then declines as housing density intensifies (Marzluff 2001). My work was focused in areas near the rural end of the housing density gradient that typically has high bird diversity due to conversion of forests to non-forest areas and increased forest edge, which increases bird habitat heterogeneity (Grime 1973). At a given patch size, Neotropical species diversity and abundance decrease with increasing housing density (Friesen et al. 1995). Forest songbird richness along North American Breeding Bird Survey (BBS) routes in forested ecosystems is negatively correlated with housing density (Pidgeon et al. 2007). Projections of bird species distributions in California suggest that rural development will limit species range expansion projected by shifting climate by as much as one-third (Jongsomjit et al. 2012).

Development is often clustered around protected areas (Wade & Theobald 2010; Davis & Hansen 2011; Mockrin et al. 2013) and this close proximity facilitates access into protected areas, particularly for recreational activities such as hiking. Participation in hiking has increased nearly 8-fold between 1960 and 2000, and occurs mostly within protected areas (Reed & Merenlender 2008). At the same time, a number of trail initiatives have been established throughout the country, with the National Trails System (NTS) being perhaps most prominent (http://www.nps.gov/nts/). Many states have their own trail initiatives as well, some of which include NTS trails. Wisconsin, for example, currently has over 2,700 miles of hiking trails within state parks and approximately 700 miles of NTS trails (http://dnr.wi.gov), as well as a State Trails Coordinator in the Department of Natural Resources (DNR). Many of Wisconsin's trails are found mostly within protected areas.

The potential benefits of protected areas include not only outdoor recreation, but clean air and water, and a place to reconnect with nature (Ostergren 2005). Outdoor recreation in protected areas is also associated with benefits to the participants (e.g. lower risk of obesity and depression in children (Louv 2008)), and economic benefits to local communities (Gössling 1999; Outdoor Industry Association 2012).

On the other hand, while the question has not been studied in depth, evidence is accumulating that the effects of recreation on birds and bird reproduction are generally negative, and in fact, of 33 papers reviewed, only five showed no effect or positive effects of recreation on bird reproductive success (Steven et al. 2011). For example, the reproductive success of Golden-cheeked Warblers (*Setophaga chrysoparia*) along mountain biking trails in Texas is half the rate of reproductive success away from trails, and is linked to habitat fragmentation and alteration due to the presence of the bike trail as well as nest abandonment near trails (Davis et al. 2010). Incubating Northern Cardinals (*Cardinalis cardinalis*) leave the nest when approached by a recreationist (Smith-Castro & Rodewald 2010). And along a heavily used trail, regular flushing can result in nest abandonment or clutch inviability due to inadequate incubation and nest attendance (Verhulst et al. 2001). Curiously, American Robins (*Turdus migratorius*) nest at higher densities near heavily used recreational trails than near infrequently used trails, but nest success is lower near the heavily used trails (Pfeiffer 2010). Acadian flycatchers exhibited an opposite pattern, avoid nesting near heavily used trails, where their nest success is low compared to nest success along infrequently used trails (Pfeiffer 2010).

Land managers have begun to consider these detrimental effects on vegetation and wildlife when planning access into protected areas, particularly in the construction of trails. Guidance documents such as *Planning Trails with Wildlife in Mind* (Trails and Wildlife Task Force 1998) and guidelines for trail placement and design from American Trails (http://www.americantrails.org) are available, but these documents are aimed at limiting erosion on trails. National Park Service trails construction guidelines specifically require trails to "[minimize] impact on the adjoining natural systems and cultural resources" (National Park Service 2004). This is laudable as a starting point to reduce ecological damage. However, it is not clear if these recommendations are adequate in achieving the concomitant goals of maintenance of high quality natural areas for wildlife protection and recreational access in protected areas.

Thus, both housing and recreational trails may negatively affect birds in protected areas, but which members of the avian community are most affected, how community patterns vary, and which mechanisms are operating are not clear. In my dissertation I address these questions in relation to both housing and recreational trails in the Baraboo Hills of southern WI, an area with increasing housing density and an extensive network of trails within protected areas.

This dissertation is divided into 3 chapters. In **chapter 1**, I examine changes in the breeding bird community in protected areas of the Baraboo Hills over 20 years. Within that time, the Baraboo Hills has experienced increased housing density (Figure 1-1). The results of this analysis suggest that the protected areas network within the Baraboo Hills has contributed to maintaining forest bird communities. In **chapter 2**, I ask whether avian community composition in forested protected areas is influenced by the physical characteristics of recreational trails, use of trails or both. Results from this analysis suggest that most forest bird species are negatively affected by trail use and width, though the width of the vegetation-free zone above trails, rather than the trail width *per se,* appears to be most negatively associated with species' densities and community composition. In **chapter 3**, I investigate the effects of trails and trail use on the reproductive success of forest passerines in protected areas. The results from this analysis suggest that, at least for some passerines, nesting near trails may be a temporal ecological trap, since nesting territories are established before trails receive their highest use, which appears to degrade habitat quality.

My work has contributed ecological knowledge and land conservation. It is generally assumed that our low-impact activities are not detrimental to the flora and fauna of a protected area, and may even serve indirectly to promote conservation. However, I showed that apparently benign activities such as hiking can alter bird community composition and reduce nesting success in large portions of a protected area. My work showed that interior forest edges, such as those found along trails, have similar ecological consequences to bird communities as do exterior edges. My work also provides a proof of concept for the idea that targeted conservation efforts can protect vulnerable habitats and their wildlife species. However, when human use of a forested protected area is allowed, trails should be narrow, and trails that were established on old roads should be restored to limit the effects of interior edge on forest bird communities.

Literature cited

Boyle SA, Samson FB. 1985. Effects of Nonconsumptive Recreation on Wildlife: A Review. Wildlife Society Bulletin **13**:110–116.

Davis CA, Leslie DM, Walter WD, Graber AE. 2010. Mountain Biking Trail Use Affects Reproductive Success of Nesting Golden-Cheeked Warblers. The Wilson Journal of Ornithology **122**:465–474.

Davis CR, Hansen AJ. 2011. Trajectories in land use change around U.S. National Parks and challenges and opportunities for management. Ecological Applications **21**:3299–3316.

Forman RTT, Alexander LE. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29**:207–231.

Friesen LE, Eagles PFJ, Mackay RJ. 1995. Effects of Residential Development on Forest-Dwelling Neotropical Migrant Songbirds. Conservation Biology **9**:1408–1414.

Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. Ecological Applications **20**:1913–1925.

Gössling S. 1999. Ecotourism: a means to safeguard biodiversity and ecosystem functions? Ecological Economics **29**:303–320.

Grime JP. 1973. Competitive exclusion in herbaceous vegetation. Nature **242**:344–347.

Hawbaker TJ, Radeloff VC, Clayton MK, Hammer RB, Gonzalez-Abraham CE. 2006. Road Development, Housing Growth, and Landscape Fragmentation in Northern Wisconsin: 1937-1999. Ecological Applications **16**:1222–1237.

Jongsomjit D, Stralberg D, Gardali T, Salas L, Wiens J. 2012. Between a rock and a hard place: the impacts of climate change and housing development on breeding birds in California. Landscape Ecology **28**:187–200.

Louv R. 2008. Last Child in the Woods: Saving Our Children From Nature-Deficit Disorder Updated and Expanded edition. Algonquin Books, Chapel Hill, N.C.

Martinuzzi S, Radeloff V, Higgins J, Helmers D, Plantinga A, Lewis D. 2013. Key areas for conserving United States' biodiversity likely threatened by future land use change. Ecosphere **4**:art58.

Marzluff JM. 2001. Worldwide urbanization and its effects on birds. Pages 19–47in J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian Ecology and Conservation in an Urbanizing World. Springer US.

Mockrin M, Stewart S, Radeloff V, Hammer R, Johnson K. 2013. Spatial and temporal residential density patterns from 1940 to 2000 in and around the Northern Forest of the Northeastern United States. Population and Environment **34**:400–419.

National Park Service. 2004. Natural Resource Management Reference Manual #77. National Park Service, U.S. Department of the Interior. Available from https://www.nature.nps.gov/rm77/ (accessed April 11, 2016).

Odell EA, Knight RL. 2001. Songbird and Medium-Sized Mammal Communities Associated with Exurban Development in Pitkin County, Colorado. Conservation Biology **15**:1143–1150.

Ostergren D. 2005. Chapter 12 Making connections: the tactics, art and science of building political support for protected natural areas. J. A. McNeely, editor. Friends for Life: New partners in support of protected areas. International Union for Conservation of Nature, Gland, Switzerland and Cambridge, UK.

Outdoor Industry Association. 2012. The Outdoor Recreation Economy. Page 20.

Parendes LA, Jones JA. 2000. Role of Light Availability and Dispersal in Exotic Plant Invasion along Roads and Streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology **14**:64–75.

Pfeiffer MJ. 2010. Effects of recreational trails on community composition and reproductive success of songbirds in southern Wisconsin forests. M.S. University of Wisconsin-Madison, Madison, WI.

Pidgeon AM, Radeloff VC, Flather CH, Lepczyk CA, Clayton MK, Hawbaker TJ, Hammer RB. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. Ecological Applications **17**:1989–2010.

Radeloff VC, Stewart SI, Hawbaker TJ, Gimmi U, Pidgeon AM, Flather CH, Hammer RB, Helmers DP. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences **107**:940–945.

Reed SE, Merenlender AM. 2008. Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. Conservation Letters **1**:146–154.

Smith-Castro JR, Rodewald AD. 2010. Behavioral responses of nesting birds to human disturbance along recreational trails. Journal of Field Ornithology **81**.

Steven R, Pickering C, Guy Castley J. 2011. A review of the impacts of nature based recreation on birds. Journal of Environmental Management **92**:2287–2294.

Trails and Wildlife Task Force. 1998. Planning Trails with Wildlife in Mind. Colorado State Parks and Hellmund Associates.

Verhulst S, Oosterbeek K, Ens BJ. 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. Biological Conservation **101**:375–380.

Wade AA, Theobald DM. 2010. Residential development encroachment on US protected areas. Conservation Biology **24**:151–161.

Wade AA, Theobald DM, Laituri MJ. 2011. A multi-scale assessment of local and contextual threats to existing and potential US protected areas. Landscape and Urban Planning **101**:215–227.

Wood EM, Pidgeon AM, Radeloff VC, Keuler NS. 2012. Image texture as a remotely sensed measure of vegetation structure. Remote Sensing of Environment **121**:516–526.

Wood EM, Pidgeon AM, Radeloff VC, Helmers DP, Culbert PD, Keuler NS, Flather CH. 2015. Long-term avian community response to housing development at the boundary of US protected areas: effect size increases with time. Journal of Applied Ecology **52**:1227–1236.

Chapter 1: Stable bird communities in the Baraboo Hills: A result of targeted conservation efforts?

1-1 Abstract

Broad-scale declines in forest bird populations have been linked to loss and fragmentation of forests and increased exurban development. Land protection is a major tool to protect bird populations, but knowing whether protection efforts are sufficient to maintain communities is not often evaluated. The Baraboo Hills is one of the largest forested areas in southern Wisconsin, and approximately 50% of the forested land area is protected from development by state agencies or non-governmental organizations. We investigated changes in forest bird communities in the Baraboo Hills between the late 1970s and the early 2000s, and the degree to which changes in land cover or development influenced bird community change. We expected to find that the area of core forest cover had decreased, while edge forest cover and housing density had increased between the 1970s and 2000s, and that species turnover had occurred between the periods due to fewer forest interior bird species and more edge affiliated and synathropic species. We found that changes in beta diversity between time periods was indeed primarily due to turnover in species composition, though

this turnover was not related to changes in forest cover or development. We did not find a significant change in edge forest cover, core forest cover or housing density. Over all plots we did not detect change in species richness for five of seven foraging and migratory guilds we examined, but did find increases in the species richness of resident and interior forest functional guilds. These increases were not strongly associated with changes in housing density or land cover. However, at some plots a decrease in Neotropical migrant species occurred, and this was associated with increased development and forest edge cover. While many bird species have declined across the U.S. in association with rural development, local conservation efforts appear to have mitigated such changes in the breeding bird community of the Baraboo Hills.

Keywords: Beta diversity, rural development, land cover change, protected areas

1-2 Introduction

There has been a substantial increase in rural development in the United States over the past 50 years (Gonzalez-Abraham et al. 2007a; Radeloff et al. 2010; Kirk et al. 2012). Development is often clustered based on accessibility to urban areas and natural features such as lakes, recreation areas, and protected areas (McGranahan 1999; Wade & Theobald 2010; Davis & Hansen 2011; Mockrin et al. 2013). However, clustering around natural features may pose a conservation conflict because these areas are often relatively high quality habitat that maintain biodiversity, while housing in close proximity erodes their biodiversity support function (Radeloff et al. 2010; Wade et al. 2011). An even greater conflict is that protected areas in the US are expected to lose 5-12% of their area by mid-century due to development (Wade & Theobald 2010; Martinuzzi et al. 2013).

Rural development, such as new housing, the expansion of farms, and associated increases in infrastructure (e.g. roads and power line), can have a number of consequences on natural communities and habitats. Rural development is associated with both fragmentation and loss of forest (e.g., in northern Wisconsin (Gonzalez-Abraham et al. 2007a, 2007b), New England (Kluza et al. 2000), and Wyoming (Smith & Wachob 2006)), while increased road density typically accompanies increased housing development, which further increases habitat fragmentation and creates corridors used by predators (Forman & Alexander 1998; Parendes & Jones 2000; Hawbaker et al. 2006). Low density housing is also correlated with increased invasive exotic plant species richness (Gavier-Pizarro et al. 2010), homogenization of native plant communities (Trentanovi et al. 2013), and changes in small mammal communities (Odell & Knight 2001).

Rural development also affects bird communities. Richness and abundance of bird species as a whole peaks near the middle of the gradient from natural area to urban center, then quickly declines with increasing urban cover as habitat specialists are lost; areas of high housing density are inhabited by just a few habitat generalists or synanthropic species (Kluza et al. 2000; Crooks et al. 2004; Fraterrigo & Wiens 2005). Synanthropic species are adapted to the simplified habitats and make use of structures associated with development, and both synanthropic and habitat generalist species often benefit from supplemental feeding in urban areas (Emlen 1974; Tryjanowski et al. 2015).

Many interior forest breeding species are Neotropical migrants that require large tracts of contiguous habitat in the breeding season (Zuckerberg & Porter 2010). Interior forest breeding species typically avoid forest edges and disturbed areas when establishing breeding territories, so perforating forests with development effectively reduces the habitat available to this group (Cooke 1980). Diversity, abundance, and reproductive success of many Neotropical migrant species, particularly ground nesting species, are lower in areas with moderate housing density compared to areas with low housing density (Friesen et al. 1995; Kluza et al. 2000; Pidgeon et al. 2007; Lepczyk et al. 2013). Projections of bird species' distribution shifts due to climate change in California suggest that anticipated rural development will reduce the area of suitable habitat by as much as one-third (Jongsomjit et al. 2013). It is clear then that rural development has a negative effect on many bird species. Housing and associated development can, therefore, affect the overall composition and diversity of avian communities through its effect on predators, fragmentation and amount of habitat.

Maintaining areas that contain critical habitat features is necessary for maintaining populations at functional levels. However, how much area needs to be protected to ensure persistence of all native species regardless of their sensitivity to human disturbance, is still a difficult question to answer. Determining the extent to which protection efforts have succeeded is challenging, but one effective approach is to compare contemporary communities with historical communities.

Here we investigated the effects of rural development on bird communities in an area where development pressure has intensified due to rich amenities and proximity to a major urban center. Our objectives were to (1) quantify forest bird communities in the late 1970s and again in the early 2000s; (2) quantify housing and homestead density (as proxies for rural development) and forest land cover patterns; and (3) investigate how changes in rural development and forest land cover have affected forest songbird composition over this time period. We expected to see a decline in forest cover and an increase in housing density between sampling periods. We further expected that these changes would be accompanied by a decrease in the richness and abundance of forest breeding birds between survey periods. We also hypothesized that overall species richness had increased between sample periods, due to increased habitat diversity from forest conversion to development and agriculture across the study area, and that bird communities would become more similar between time periods due to development.

1-3 Methods

1-3.1 Study area

Our study area is the Baraboo Hills of southern Wisconsin, USA (Figure 1-1). The Baraboo Hills is one of the largest forested areas in southern Wisconsin, with approximately 22,000 ha of primarily deciduous forest. The forests are primarily southern hardwood forest, dominated by white oak (Quercus alba), basswood (Tillia americana), and bitternut hickory (Carya cordiformis), and members of the northern mesic forest such as white pine (Pinus strobus), eastern hemlock (Tsuga canadensis) and yellow birch (Betula alleghaniensis) (Curtis 1959). The climate of the region is classified as humid continental, characterized by large seasonal variation in temperature (Peel et al. 2007). The long-term average temperature for the summer (May-August) is 18.6C and average precipitation is 9.0 cm (National Oceanic and Atmospheric Administration 2016).

The Baraboo Hills contain numerous protected areas, many established in the last 50 years to preserve the unique habitats of the region. State of Wisconsin-owned protected areas total approximately 5,500 ha (http://dnr.wi.gov), while The Nature Conservancy, a private conservation organization, manages approximately 5,000 ha as natural areas in the Baraboo Hills (http://www.nature.org). The Baraboo Hills contain two urban areas, the cities of Baraboo (2010 population: 12,048) and Reedsburg (2010 population: 10,014), as well as numerous small towns and unincorporated villages. Rural development is increasing in the area due, at least in part, to its proximity to Madison, the state capitol, which is approximately 80 km to the southeast (Radeloff et al. 2010; U.S. Census Bureau 2012; Figure 1-1).

1-3.2 Avian community composition

We surveyed forest bird communities at 18 forested plots in the Baraboo Hills during the breeding seasons of 1977-1979 (herein, the 1970s) and these were resurveyed during the breeding seasons of 1998-2003 (herein, the 2000s). Each transect was surveyed once per sampling period. The surveys were conducted between sunrise and 10:00 am during favorable weather conditions. We established variable length transects (range: 0.40-2.27 km, mean = 1.26 km) through relatively homogeneous habitat in each plot, recording all birds seen or heard along the transect. We used an unbounded strip transect method during bird surveys, without distance estimation, a common method for avian community sampling in the 1970s.

We used transect-level relative abundance as our independent variable in species- and guild-level analyses. To calculate relative abundance, we first standardized counts of each species by transect length (#observed/km). Then we divided the standardized count by the sum of the standardized counts of all species within a transect. To calculate relative abundance of guilds, we summed the relative abundance of all guild member species. We calculated relative abundance of migrant guilds (i.e. Neotropical, short-distance, resident), nest location guilds (i.e. interior forest nesting, ground nesting, cavity nesting), and synanthropes (Peterjohn & Sauer 1993; Pidgeon et al. 2014). These guild types are not mutually exclusive, meaning that a species may belong to more than one guild type (Appendix 1-1).

1-3.3 Housing and land cover

We used 1:40,000 scale leaf-on, black and white georectified orthophotos from 1978 and 2001 in a GIS to locate all structures and homesteads within 1 km of forest bird transects. We calculated the density of homesteads within 250 m (homestead density) and density of structures within 1 km (structure density) for each sampling period. We chose to investigate homestead density within 250 m of the transect because homesteads alter forest habitat by removing forest cover, and/or by altering the balance of resources available to different avian guilds through, for example, supplemental feeding and planting of fruit-producing ornamental woody plants. Structures might also provide refugia for mesopredators (e.g. domestic cats (*Felis catus*)) that are able to travel relatively long distances to hunt (relevant in both 250 m and 1 km scale landscapes). We digitized forest land cover using a majority rule within a 30 m minimum mapping unit from 1978 aerial photographs to quantify forest cover during the

1970s and used the 2001 National Land Cover Database (NLCD; Jin et al. 2013) to determine forest cover during the 2000s. The minimum mapping unit was selected so that forest cover amount would be directly comparable in the two sampling periods. We used morphological spatial pattern analysis (Vogt et al. 2007) to obtain the percent edge forest (defined as the exterior 60 m of a forest patch) within 250 m of a transect. This edge width was chosen based on evidence that the abundance of several forest songbird species found in the Baraboo Hills is lower within 60 m of forest edge (Kroodsma 1984). We also characterized the percent of core forest within 2 km of each transect, since the abundance of many forest bird species is related to the amount of forest within the landscape (Andrén 1994). We calculated changes in structure density, homestead density, core forest, and edge forest between the 1970s and 2000s. For each transect, we calculated change by subtracting the value of a particular landscape metric in the 2000s from the value of the same metric in the 1970s. We also calculated absolute pair-wise differences in structure density, homestead density, core forest cover and edge forest cover for each transect pair within sampling periods.

1-3.4 Statistical analysis

We used nonmetric multidimensional scaling (NMDS) to investigate patterns of avian community composition among plots in each sampling period and between sampling periods. We fit environmental variables the ordination to investigate how patterns of community composition and species abundance are associated with our landscape variables. We used a Bray-Curtis dissimilarity matrix of the square-root transformed species×plot abundance matrix in the ordination (McCune et al. 2002). We also tested for differences in avian communities between sampling periods using analysis of similarity (ANOSIM), using 999 Monte Carlo simulations to generate the AMOSIM *R* statistic (Clarke 1993). ANOSIM *R* ranges from zero to one; zero indicates that the communities are identical, and one indicates the communities are completely different.

We investigated whether patterns in beta diversity within and between sampling periods were related to forest cover and housing density. Beta diversity calculated using presence/absence data can be decomposed into two components: nestedness (gain or loss in species) and turnover (species replacement), and, when calculated using abundance data, the analogous components are gradient (change in proportional species representation) and balanced variation (species replacement) (Baselga 2010, 2013). Examining these components of beta diversity individually allowed us to refine our understanding of the mechanism(s) by which land cover and/or housing density influence the bird community. We calculated pair-wise presence/absence-based

Søreneson dissimilarity between time periods and abundance-based beta diversity indices for avian communities using the Bray-Curtis dissimilarity index between transects within sampling periods (Baselga 2010, 2013).

We used Bayesian model averaging with generalized linear models to investigate whether plot level pair-wise differences in structure density, homestead density, and land cover contributed to abundance-based dissimilarity, nestedness, and turnover within a sampling period. Bayesian model averaging provides improved predictive power compared to frequentist model averaging by accounting for uncertainty in the model selection process (Raftery 1995; Hoeting et al. 1999). We used the BIC approximation for model selection, wherein models included in the average had BIC < 6 and had no nested submodels with a lower BIC (Raftery 1995). Bayesian model averaging provides an estimated parameter value (EV), the standard deviation for each EV from the selected models (SD), and the posterior probability that each EV is not equal to zero ($P_{\neq 0}$). We also investigated whether the relative abundance of guilds was related to structure density, homestead density, core forest cover, or edge forest cover within a sampling period and whether changes in community structure between sampling periods was related to changes in landscape metrics between sampling periods using Bayesian model averaging. We logit transformed relative abundance (Warton & Hui 2011) and scaled and centered all independent variables prior to analysis. All analyses were completed in the R statistical environment (R Core Development Team 2013).

1-4 Results

The amount of core forest cover and edge forest cover remained stable between the late 1970s and 2000s, as did homestead density within 250m and structure density within 1 km of transects (two-sample t-test: $P > 0.05$, Table 1-1; Figure 1-2). Highest species richness and relative abundance were found within the Neotropical migrant guild in both sampling periods (species richness = 10.39 [SE 1.02] and 11.61 [0.91], relative abundance = 0.57 [0.03] and 0.64 [0.03] in the 1970s and 2000s respectively; Table 1-2; Figure 1-3), while lowest species richness and relative abundance occurred in the synanthrope guild (species richness = 2.11 [0.25] and 2.67 [0.30], relative abundance = 0.13 [0.25] and 0.07 [0.01] in the 1970s and 2000s respectively; Table 1-2; Figure 1-3).

The relative abundance of all guilds remained stable across the study area between the 1970s and the 2000s (two-sample t-test: $P > 0.05$, Figure 1-3a). Individual transects did show change in the relative abundance of some guilds, however (Figure 1-3a). Resident and interior species richness increased across the study area between sampling periods (two-sample t-test: $P < 0.05$; Figure 1-3b), while species richness of the other guilds, and overall species richness, did not change across the study area (two-sample t-test: $P > 0.05$; Figure 1-3b).

The final 2-axis NMS solution had a stress of 0.19, indicating a good representation of the original 76-dimension community. The second axis was primarily negatively correlated with core forest area ($r = -0.98$, $P < 0.001$, Figure 1-4), while the first axis was not strongly correlated with any of our measured variables. Differences in bird community composition between years were primarily associated with axis 1, and bird communities were more similar to each other in the 2000s than in the 1970s (ANOSIM: $R = 0.08$, $P < 0.05$; Figure 1-4). Differences in forest guild associations fell along axis 1, with interior forest species typically being negatively associated with axis 1, while all other species were typically positively associated with axis 1 (Figure 1-5).

Within-sampling period pairwise abundance-based dissimilarities were primarily due to differences in balance (i.e., different species occurred in different plots). Pair-wise balance was not strongly associated with any pair-wise differences in landscape variables within the 1970s, but was negatively associated with differences in housing density in the 2000s (BMA: estimated value (EV) = -0.01 [SD 0.01], $P_{\neq 0} = 0.68$; Figure 1-6).

The relative abundance of ground nesting species in the 1970s was negatively associated with amount of edge forest cover within 250 m (BMA: EV = -1.06 [0.39], $P_{\neq 0}$ = 1.00; Figure 1-7) and the interaction between edge forest cover and homestead density (BMA: EV = -0.78 [68], $P_{\neq 0}$ = 0.72; Figure 1-7). The relative abundance of both cavity-nesting species and resident species was positively associated with homestead density in the 1970s (BMA: EV = 0.33 [0.11] and 0.23 [0.20], $P_{\neq 0}$ = 1.00 and 0.70, respectively; Figure 1-7). Resident species relative abundance was negatively associated with amount of core forest cover in the 1970s (BMA: EV = -0.19 [0.17], $P_{\neq 0}$ = 0.70; Figure 1-7).

The relative abundance of cavity-nesting species was positively associated with amount of edge forest cover (BMA: EV = 0.14 [0.13], $P_{\neq 0}$ = 0.66; Figure 1-7) in the 2000s, but not in the 1970s. Resident species relative abundance was negatively associated with amount of core forest cover (BMA: EV = -0.22 [0.20], $P_{\neq 0}$ = 0.66; Figure 1-7), while forest interior species relative abundance was negatively associated with amount of edge forest cover (BMA: EV = -0.50 [0.25], $P_{\neq 0}$ = 0.93; Figure 1-7).

Plot-level differences in the relative abundance of cavity-nesting species between sampling periods were positively associated with the interaction between the change in homestead density and the change in edge forest cover

(BMA: EV = 0.04 [0.03], $P_{\neq 0}$ = 0.76; Figure 1-7), while the difference in relative abundance of short distance migrants between the 1970s and the 2000s was positively associated with change in edge forest cover (BMA: EV = 0.06 [0.03], $P_{\neq 0}$ = 0.94; Figure 1-7) and positively associated with change in structure density (BMA: EV = 0.03 [0.03], $P_{\neq 0}$ = 0.64; Figure 1-7).

The difference in Neotropical migrant species richness between sampling periods was negatively associated with the interaction between the changes in homestead density and edge forest cover (BMA: EV = -4.32 [1.27], $P_{\neq 0}$ = 1.00; Figure 1-8). Neotropical species richness was relatively stable where changes in homestead density × edge forest cover were negative or stable, but decreased where the interaction was positive (Appendix 1-2). Plot-level differences in ground nesting species richness from the 1970s to the 2000s was positively related to the change in edge forest cover (BMA: EV = 1.37 [0.58], $P_{\neq 0}$ = 0.97; Figure 1-8). We found no relationship between our predictor variables and change in richness of the other five guilds (Appendix 1-3).

Beta diversity between sampling periods was primarily due to species turnover (Figure 1-9), however turnover between sampling periods was not associated with changes in the landscape variables we analyzed (Figure 1-9). The nestedness component of beta diversity between sampling periods was negatively associated with lower homestead density (BMA: EV = -0.01 [0.01], $P_{\neq 0}$ = 0.68; Figure 1-10) and the interaction between homestead density and edge forest cover (BMA: EV = -0.041 [0.02], $P_{\neq 0}$ = 0.90; Figure 1-10).

1-5 Discussion

We found that bird communities, forest land cover, and housing density across the 18 plots we surveyed within the Baraboo Hill were all relatively stable between the late 1970s and early 2000s. This contrasts with state- and nation-wide patterns in forest bird community trends and housing growth over similar time periods (Wisconsin: Ambuel & Temple 1983; Hawbaker et al. 2006; National: Alig et al. 2004; Radeloff et al. 2005; Pidgeon et al. 2007, 2014; Wood et al. 2015). Within our study area, approximately 16% of the area within 2 km of transects has protected status (US Geological Survey (USGS) Gap Analysis Program (GAP) 2012), which may account for these stable patterns.

We did, however, detect patterns in guild abundance within sampling periods. Consistent with our expectations, ground nesting and interior forest species were negatively associated with amount of edge forest, while resident species were negatively associated with amount of core forest, similar to findings in other forested areas in North America (Ambuel & Temple 1983; Lynch & Whigham 1984; Freemark & Merriam 1986; Askins et al. 1987).

While turnover (species replacement) was the primary component responsible for beta diversity in avian communities between time periods, overall this represented little change in forest bird communities between sampling periods. Species turnover among plots both within and between sampling periods is likely due to habitat heterogeneity. A few of the plots were located in forest that was recently re-established in the 1970s and differed structurally from the more mature forests of other plots sampled during the 1970s. These recently re-established forest plots also exhibited relatively strong changes in stand characteristics between sampling periods due to ecological succession, and were a major source of differences in bird species composition. Thus, habitat conditions related to succession, such as stem density or tree size, might be correlated with axis 1 in our ordination, though we do not have measurements for this. For example as vegetation structure in the plots changed over the ~3 decades of our study, bird species affiliated with early-successional forest were lost, including Eastern Towhee (*Pipilo erythrophthalmus*), Gray Catbird (*Dumetella carolinensis*), and Gold-winged Warbler (*Vermivora chrysoptera*) and interior forest species were added, including Red-eyed Vireo (*Vireo olivaceus*) and Ovenbird (*Seiurus aurocapilla*) (Appendix 1-4).

Plot-level differences in the abundance of both cavity nesting species and resident species were positively associated with increased edge forest cover, similar to findings for the conterminous United States (Pidgeon et al. 2014). These two guilds share many species (e.g., Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Black-capped Chickadee (*Poecile atricapillus*), and Tufted Titmouse (*Baeolophus bicolor*)), and the majority benefit from supplemental feeding associated with rural housing (Morneau et al. 1999). Development in forested areas necessarily reduces forest cover, which can result in increased edge forest (Nilon et al. 1995). Plot-level change in Neotropical migrant species richness was negatively associated with change in homestead density and edge forest cover. This is in line with other studies that have linked declines in habitat suitability for Neoptropical migrants to forest loss and rural development (Friesen et al. 1995; Pidgeon et al. 2014).

While change in edge forest area was not significant across sampled plots between periods, generally there appears to be greater gain in edge forest than loss of core forest, suggesting that fragmentation may be increasing very slowly in the Baraboo Hills, while the total area of forest habitat has remaining consistent. This increase in fragmentation may be linked to the trend of increasing housing density across the Baraboo Hills, though the trend was not significant in our sampled area. Our results are in line with other studies' findings that habitat loss is a greater driver of species' decline and loss than habitat fragmentation (Fahrig 1997). Taken together, our findings suggest that conservation efforts in the region are successfully protecting core forest areas necessary for Neotropical and interior forest bird populations to persist.

There is a history of strong land protection in the Baraboo Hills, with both local (e.g. the Baraboo Range Preservation Association) and international (e. g., The Nature Conservancy) land trusts operating in the area. Local habitat protection appears to be sufficient to maintain populations of bird species sensitive to development e.g., ground nesting and forest interior Neotropical migrants), despite evidence of nation-wide declines in these guilds associated with housing development, habitat loss and fragmentation (Andrén 1994; Pidgeon et al. 2007; Wood et al. 2015).

1-6 Literature cited

Alig RJ, Kline JD, Lichtenstein M. 2004. Urbanization on the US landscape: looking ahead in the 21st century. Landscape and Urban Planning **69**:219–234.

Ambuel B, Temple SA. 1983. Area-Dependent Changes in the Bird Communities and Vegetation of Southern Wisconsin Forests. Ecology **64**:1057–1068.

Andrén H. 1994. Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos **71**:355–366.

Askins RA, Philbrick MJ, Sugeno DS. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. Biological Conservation **39**:129–152.

Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography **19**:134–143.

Baselga A. 2013. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. Methods in Ecology and Evolution **4**:552–557.

Clarke K. 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology **18**:117–143.

Cooke AS. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biological Conservation **18**:85–88.

Crooks KR, Suarez AV, Bolger DT. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation **115**:451–462.

Davis CR, Hansen AJ. 2011. Trajectories in land use change around U.S. National Parks and challenges and opportunities for management. Ecological Applications **21**:3299–3316.

Emlen JT. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. The Condor **76**:184–197.

Fahrig L. 1997. Relative Effects of Habitat Loss and Fragmentation on Population Extinction. The Journal of Wildlife Management **61**:603–610.

Forman RTT, Alexander LE. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29**:207–231.

Fraterrigo JM, Wiens JA. 2005. Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. Landscape and Urban Planning **71**:263–275.

Freemark KE, Merriam HG. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation **36**:115–141.

Friesen LE, Eagles PF, Mackay R. 1995. Effects of Residential Development on Forest-Dwelling Neotropical Migrant Songbirds. Conservation Biology **9**:1408–1414.

Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. Ecological Applications **20**:1913–1925.

Gonzalez-Abraham CE, Radeloff VC, Hammer RB, Hawbaker TJ, Stewart SI, Clayton MK. 2007a. Building patterns and landscape fragmentation in northern Wisconsin, USA. Landscape Ecology **22**:217–230.

Gonzalez-Abraham CE, Radeloff VC, Hawbaker TJ, Hammer RB, Stewart SI, Clayton MK. 2007b. Patterns of Houses and Habitat Loss from 1937 to 1999 in Northern Wisconsin, USA. Ecological Applications **17**:2011–2023.

Hawbaker TJ, Radeloff VC, Clayton MK, Hammer RB, Gonzalez-Abraham CE. 2006. Road development, housing growth, and landscape fragmentation in northern Wisconsin: 1937-1999. Ecological Applications **16**:1222–1237.

Hoeting JA, Madigan D, Raftery AE, Volinsky CT. 1999. Bayesian Model Averaging: A Tutorial. Statistical Science **14**:382–401.

Jin S, Yang L, Danielson P, Homer C, Fry J, Xian G. 2013. A comprehensive change detection method for updating the National Land Cover Database to circa 2011. Remote Sensing of Environment **132**:159–175.

Jongsomjit D, Stralberg D, Gardali T, Salas L, Wiens J. 2013. Between a rock and a hard place: the impacts of climate change and housing development on breeding birds in California. Landscape Ecology **28**:187–200.

Kirk RW, Bolstad PV, Manson SM. 2012. Spatio-temporal trend analysis of long-term development patterns (1900–2030) in a Southern Appalachian County. Landscape and Urban Planning **104**:47–58.

Kluza DA, Griffin CR, Degraaf RM. 2000. Housing developments in rural New England: effects on forest birds. Animal Conservation **3**:15–26.

Kroodsma RL. 1984. Effect of Edge on Breeding Forest Bird Species. The Wilson Bulletin 96:426–436.

Lepczyk CA, Wunnicke A, Radeloff VC, Flather CH, Pidgeon AM, Hammer RB. 2013. Using housing growth to estimate habitat change: detecting Ovenbird response in a rapidly growing New England State. Urban Ecosystems **16**:1–12.

Lynch JF, Whigham DF. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation **28**:287–324.

Martinuzzi S, Radeloff V, Higgins J, Helmers D, Plantinga A, Lewis D. 2013. Key areas for conserving United States' biodiversity likely threatened by future land use change. Ecosphere **4**:art58.

McCune B, Grace JB, Urban DL. 2002. Analysis of ecological communities. MjM Software Design. Gleneden Beach, Oregon.

McGranahan DA. 1999. Natural Amenities Drive Rural Population Change. Agricultural Economics Reports 33955. United States Department of Agriculture, Economic Research Service. Available from https://ideas.repec.org/p/ags/uerser/33955.html (accessed April 17, 2016).

Mockrin M, Stewart S, Radeloff V, Hammer R, Johnson K. 2013. Spatial and temporal residential density patterns from 1940 to 2000 in and around the Northern Forest of the Northeastern United States. Population and Environment **34**:400–419.

Morneau F, Décarie R, Pelletier R, Lambert D, DesGranges J-L, Savard J-P. 1999. Changes in breeding bird richness and abundance in Montreal parks over a period of 15 years. Landscape and Urban Planning **44**:111–121.

National Oceanic and Atmospheric Administration. 2016. National Centers for Environmental Information. Available from https://www.ncei.noaa.gov/ (accessed April 17, 2016).

Nilon CH, Long CN, Zipperer WC. 1995. Effects of wildland development on forest bird communities. Landscape and Urban Planning **32**:81–92.

Odell EA, Knight RL. 2001. Songbird and Medium-Sized Mammal Communities Associated with Exurban Development in Pitkin County, Colorado. Conservation Biology **15**:1143–1150.

Parendes LA, Jones JA. 2000. Role of Light Availability and Dispersal in Exotic Plant Invasion along Roads and Streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology **14**:64–75.

Peel MC, Finlayson BL, Mcmahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences Discussions **4**:439–473.

Peterjohn BG, Sauer JR. 1993. North American Breeding Bird Survey annual summary 1990-1991. Bird Populations **1**:52–67.

Pidgeon AM, Flather CH, Radeloff VC, Lepczyk CA, Keuler NS, Wood EM, Stewart SI, Hammer RB. 2014. Systematic Temporal Patterns in the Relationship Between Housing Development and Forest Bird Biodiversity. Conservation Biology **28**:1291–1301.

Pidgeon AM, Radeloff VC, Flather CH, Lepczyk CA, Clayton MK, Hawbaker TJ, Hammer RB. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. Ecological Applications **17**:1989–2010.

R Core Development Team. 2013. R: A Language and Environment for Statistical Computing. Vienna, Austria. Available from http://www.R-project.org/.

Radeloff VC, Hammer RB, Stewart SI. 2005. Rural and Suburban Sprawl in the U.S. Midwest from 1940 to 2000 and Its Relation to Forest Fragmentation. Conservation Biology **19**:793–805.

Radeloff VC, Stewart SI, Hawbaker TJ, Gimmi U, Pidgeon AM, Flather CH, Hammer RB, Helmers DP. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences **107**:940–945.

Raftery AE. 1995. Bayesian model selection in social research. Sociological methodology **25**:111–164.

Smith CM, Wachob DG. 2006. Trends associated with residential development in riparian breeding bird habitat along the Snake River in Jackson Hole, WY, USA: Implications for conservation planning. Biological Conservation **128**:431–446.

Trentanovi G, Lippe M, Sitzia T, Ziechmann U, Kowarik I, Cierjacks A. 2013. Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion. Diversity and Distributions **19**:738–748.

Tryjanowski P et al. 2015. Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. Environmental Science and Pollution Research **22**:15097–15103.

U.S. Census Bureau. 2012. 2010 Census of Population and Housing, Summary Population and Housing Characteristics, CPH-1-51, Wisconsin. U.S. Government Printing Office, Washington, DC.

US Geological Survey Gap Analysis Program (GAP). 2012, November 30. Protected Areas Database of the United States (PADUS) version 1.3. USGS Gap Analysis

Program (GAP). Available from http://gapanalysis.usgs.gov/PADUS (accessed December 15, 2013).

Vogt P, Riitters KH, Estreguil C, Kozak J, Wade TG. 2007. Mapping spatial patterns with morphological image processing. Landscape Ecology **22**:171–177.

Wade AA, Theobald DM. 2010. Residential development encroachment on US protected areas. Conservation Biology **24**:151–161.

Wade AA, Theobald DM, Laituri MJ. 2011. A multi-scale assessment of local and contextual threats to existing and potential US protected areas. Landscape and Urban Planning **101**:215–227.

Warton DI, Hui FKC. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology **92**:3–10.

Wood EM, Pidgeon AM, Radeloff VC, Helmers DP, Culbert PD, Keuler NS, Flather CH. 2015. Long-term avian community response to housing development at the boundary of US protected areas: effect size increases with time. Journal of Applied Ecology **52**:1227–1236.

Zuckerberg B, Porter WF. 2010. Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. Biological Conservation **143**:952–962.

1-7 Tables

Table 1-1 Summary of landscape variables within each sampling period, and t-test results for between sampling periods. There was no statistical difference for any variable between time periods (T-test, df = 18, α = 0.05).

Variable	1970s	2000s	t-statistic
Core forest (2 km)	0.43 (0.06)	0.42 (0.05)	0.16
Edge forest (250 m)	0.14 (0.03)	0.19 (0.03)	-1.28
Homestead density (250 m)	0.01 (0)	0.01 (0)	-0.25
Structure density (1 km)	0.05 (0.01)	0.06 (0.01)	-0.97

Table 1-2 Guild richness and relative abundance within sampling periods. Columns under t-test show the t-statistic comparing richness and relative abundance between time periods. (T-test, df = 18, $\alpha = 0.05$).

	1970s		2000s		t-statistic	
Guild	Richness	Relative abundance	Richness	Relative abundance	Richness[a]	Relative abundance
Resident	4.22 (0.43)	0.16 (0.01)	5.56 (0.36)	0.14 (0.02)	2.36*	-1.13
Short Distance migrant	6.28 (0.5)	0.26 (0.03)	6.61 (0.67)	0.22 (0.02)	0.4	0.59
Neotropical migrant	10.39 (1.02)	0.57 (0.03)	11.61 (0.91)	0.64 (0.03)	0.9	0.08
Interior forest	6.33 (0.66)	0.41 (0.04)	8.89 (0.8)	0.46 (0.05)	2.46*	-1.40
Cavity-nesting	5.11 (0.61)	0.19 (0.01)	6.39 (0.53)	0.14 (0.02)	1.58	-0.02
Ground nesting	3.67 (0.48)	0.2 (0.03)	4.28 (0.49)	0.19 (0.02)	0.89	-0.30
Synanthrope	2.11 (0.25)	0.13 (0.02)	2.67 (0.3)	0.07 (0.01)	1.41	-0.52
All species	38.11 (2.9)	1.00	46 (2.85)	1.00	1.94	--[b]

[a] t-statistic for test between 1970s and the 2000s

[b] The relative abundance of all species within a plot = 1. This is not testable by a t-test

* indicates significant difference between sampling periods ($p < 0.05$)

1-8 List of Figures

Figure 1-9 Patterns in temporal beta diversity within each sampled location between sampling periods. Temporal patterns in beta diversity were primarily driven by turnover (i.e. species replacement).

Figure 1-10 Parameter estimates of Bayesian model averaging for temporal beta diversity patterns. Circle size represents the probability a predictor variable does not equal zero ($P_{\neq 0}$). Error bars represent one standard deviation of the estimated value for the predictor.

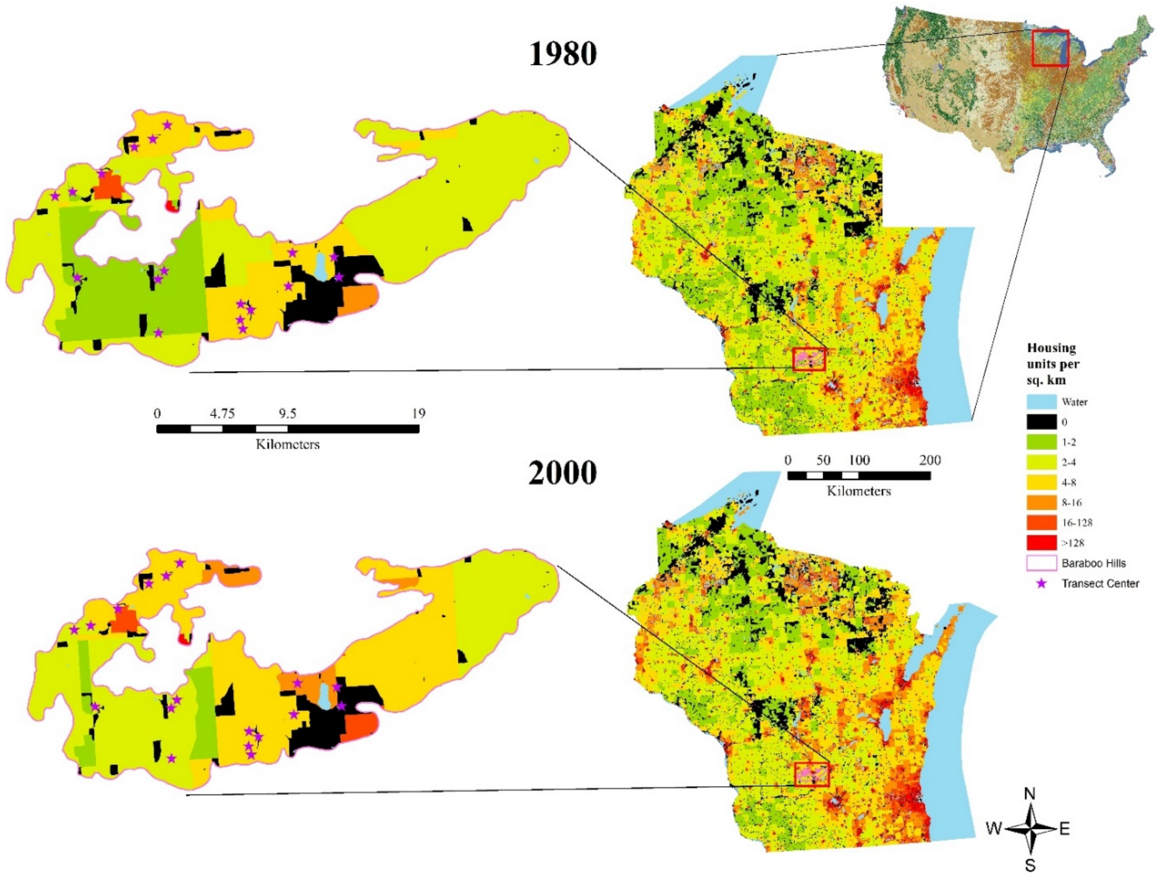

1980
2000
0 4.75 9.5 19
Kilometers
0 50 100 200
Kilometers
Housing units per sq. km
Water
0
1-2
2-4
4-8
8-16
16-128
>128
Baraboo Hills
Transect Center
N
W
E
S

Figure 1-1

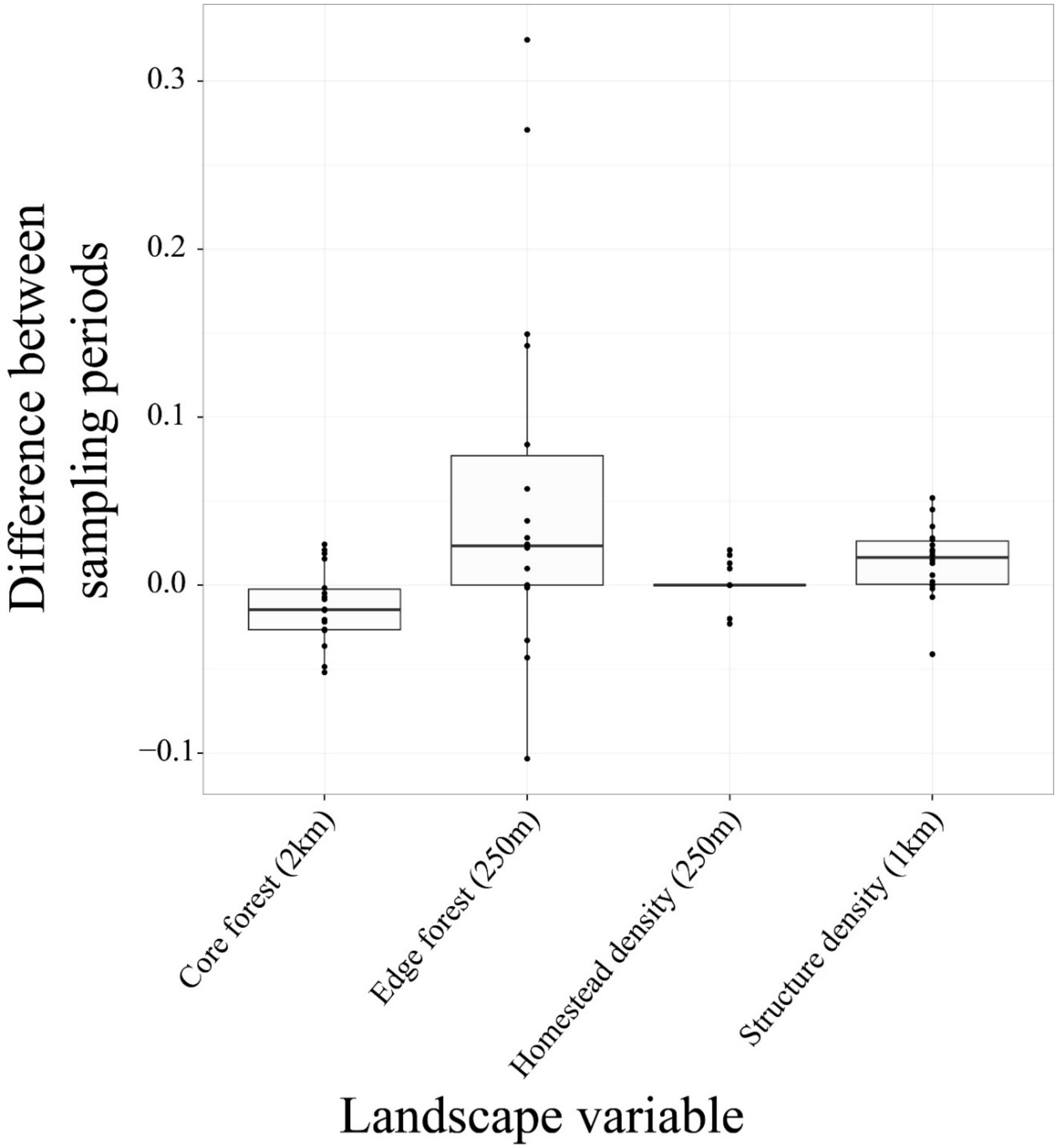

Difference between sampling periods
0.3
0.2
0.1
0.0
−0.1
Core forest (2km)
Edge forest (250m)
Homestead density (250m)
Structure density (1km)
Landscape variable

Figure 1-2

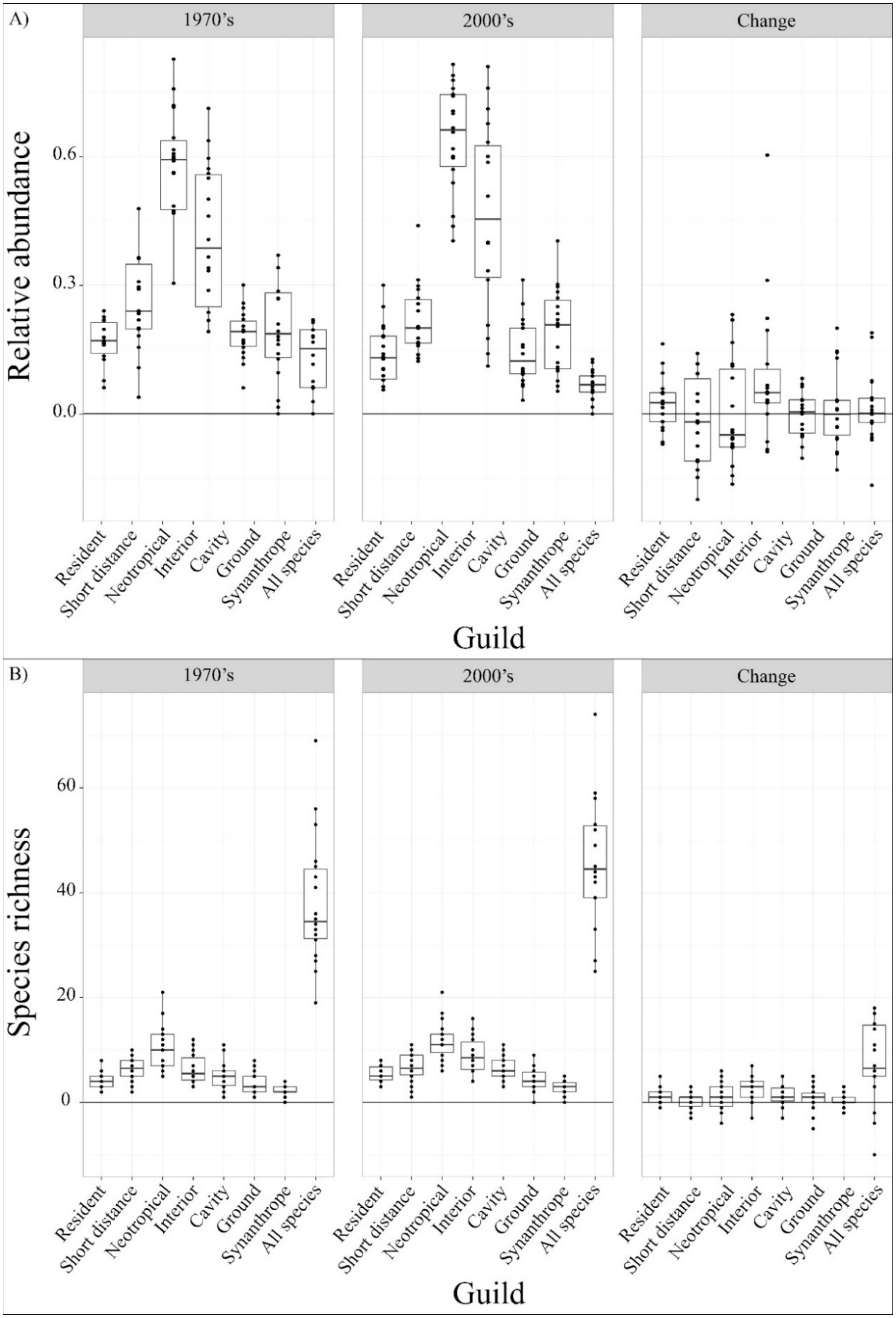

A)
1970's
2000's
Change
Relative abundance
0.0
0.3
0.6
Resident
Short distance
Neotropical
Interior
Cavity
Ground
Synanthrope
All species
Guild
B)
1970's
2000's
Change
Species richness
0
20
40
60
Resident
Short distance
Neotropical
Interior
Cavity
Ground
Synanthrope
All species
Guild

Figure 1-3

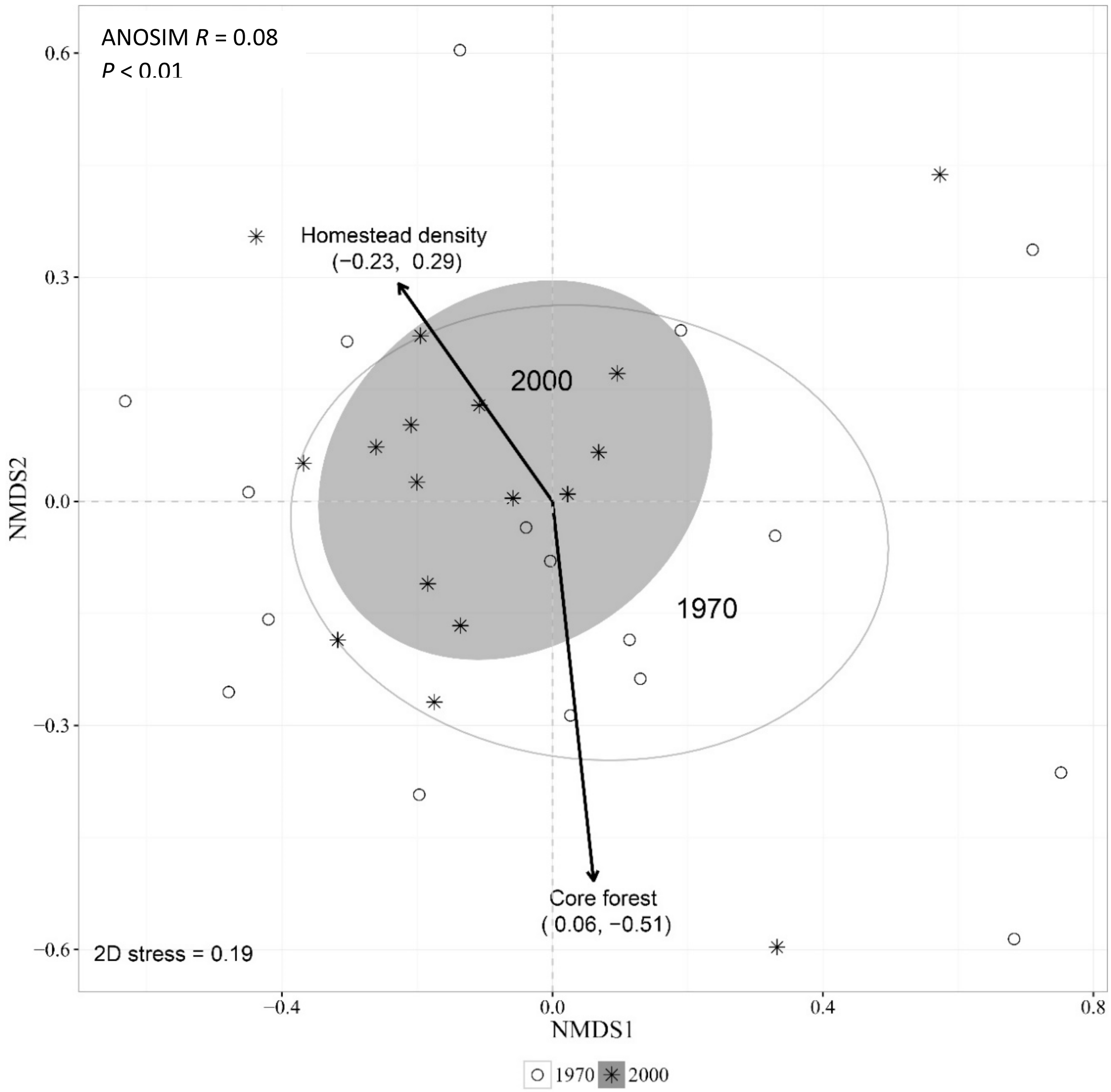

ANOSIM R = 0.08
P < 0.01
Homestead density
(−0.23, 0.29)
2000
1970
Core forest
(0.06, −0.51)
2D stress = 0.19
NMDS2
NMDS1
0.6
0.3
0.0
−0.3
−0.6
−0.4
0.0
0.4
0.8
1970
2000

Figure 1-4

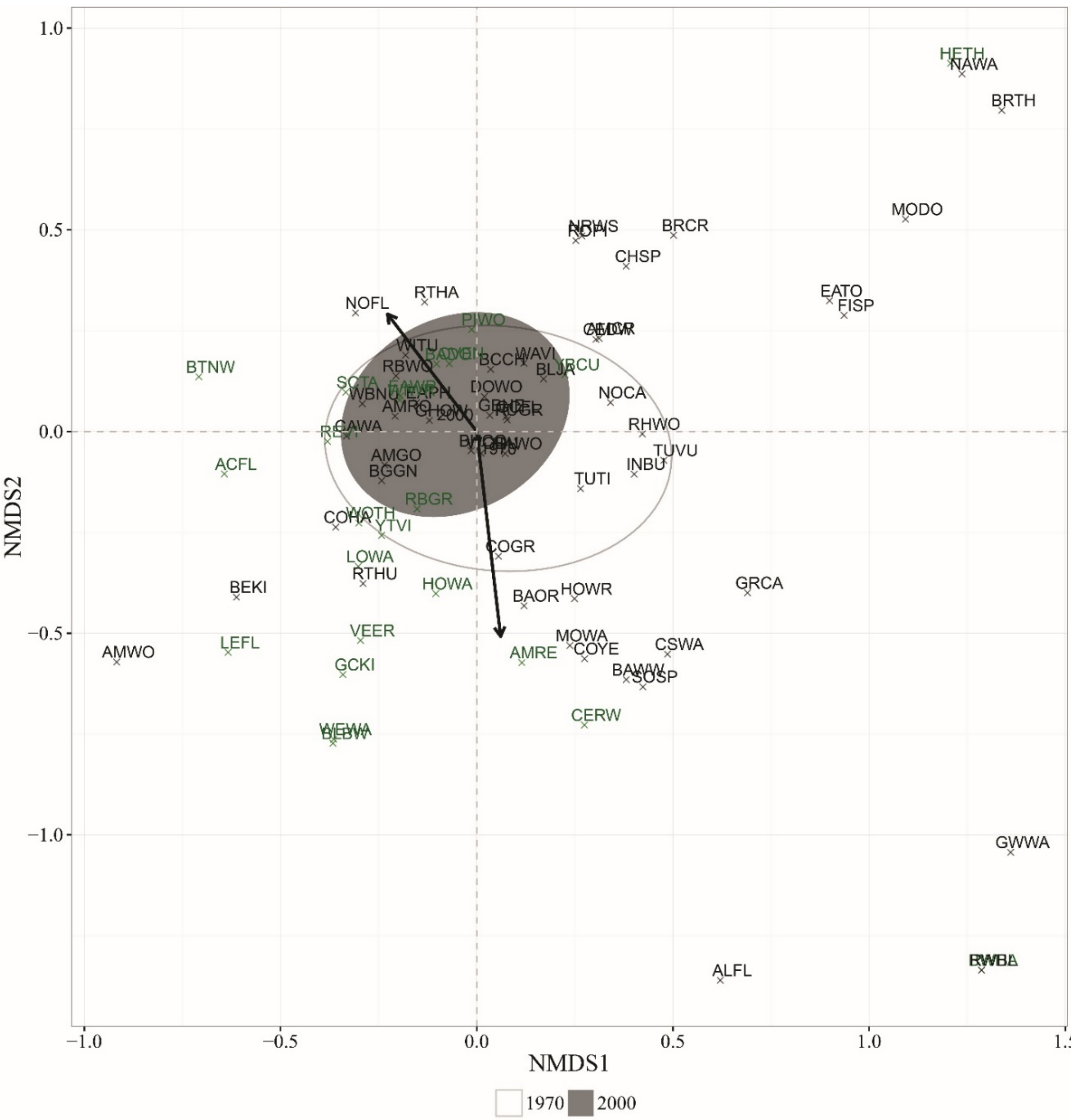

NMDS1
NMDS2
1970
2000
NOFL
RTHA
BTNW
ACFL
AMWO
BEKI
LEFL
VEER
GCKI
COGR
BAOR
HOWR
GRCA
MOWA
COYE
CSWA
AMRE
SOSP
CERW
GWWA
ALFL
MODO
BRCR
CHSP
EATO
FISP
BRTH
NAWA
HETH
NOCA
RHWO
TUVU
INBU
TUTI
AMGO
BGGN
RBGR
COHA
WOTH
YTVI
LOWA
RTHU
HOWA
PIWO
BCCH
WAVI
BLJA
DOWO
RBWO
WBNU
AMRO
CAWA
SCTA
WITU

Figure 1-5

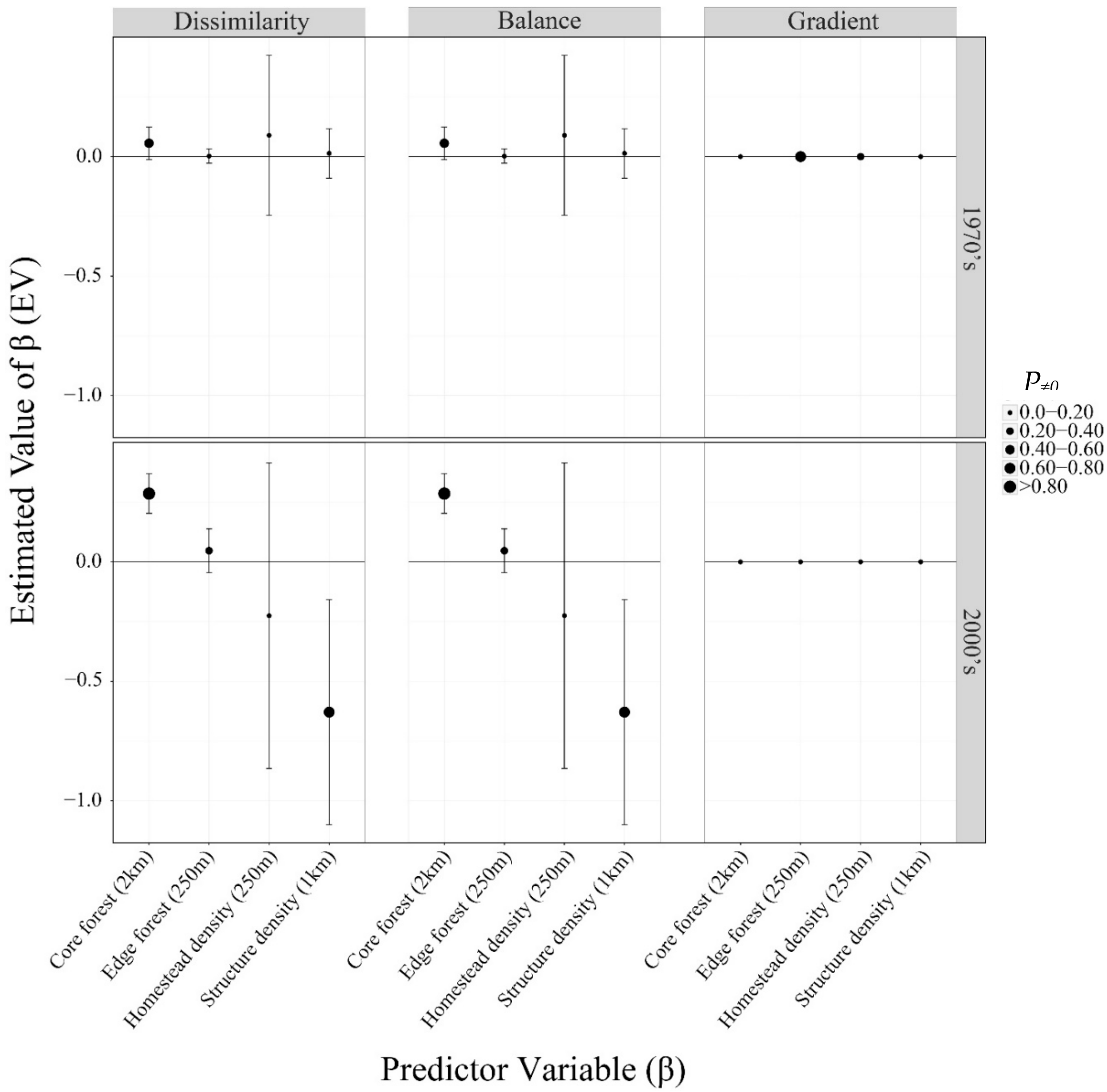
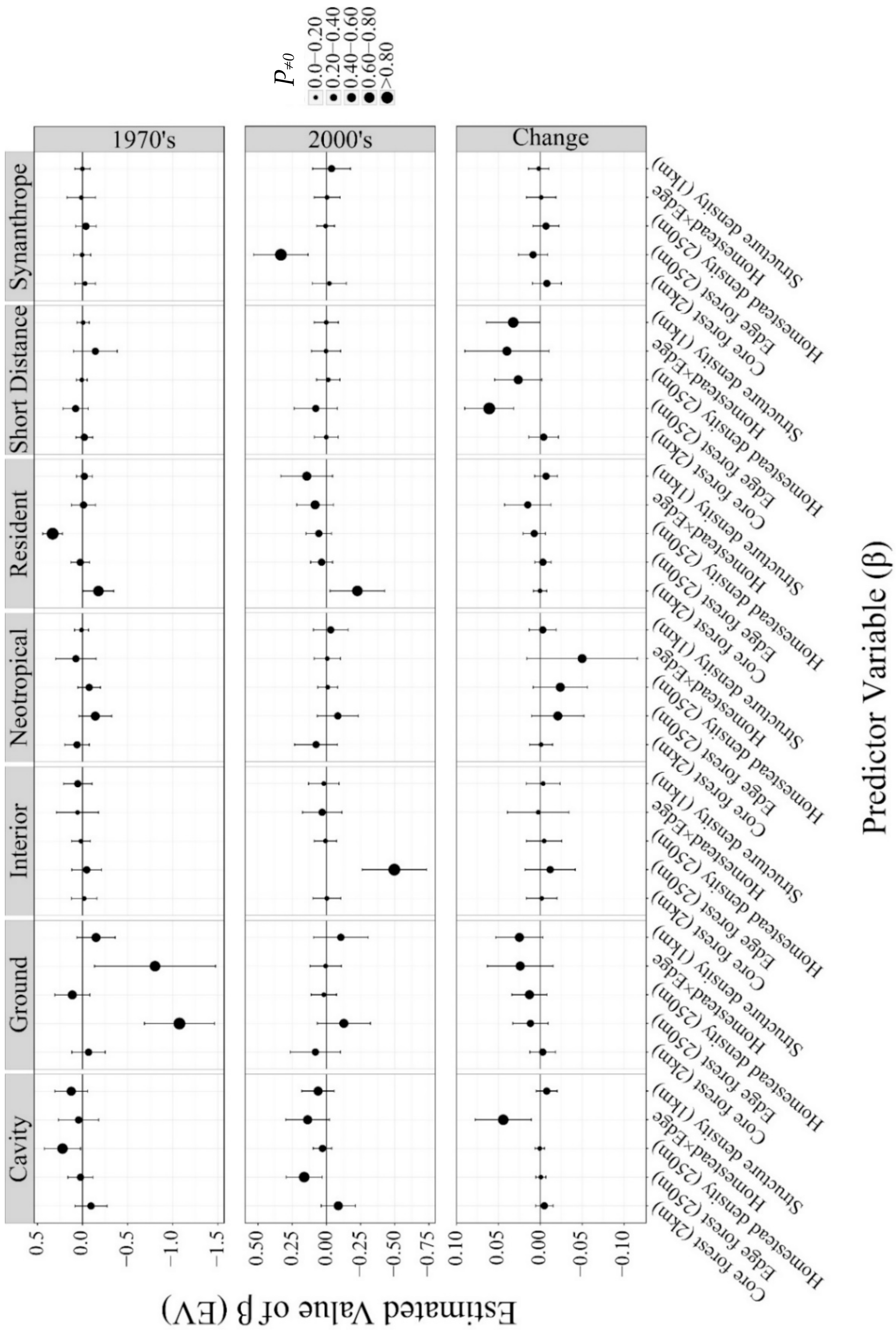

Dissimilarity
Balance
Gradient
1970's
2000's
0.0
−0.5
−1.0
Estimated Value of β (EV)
$P_{\neq 0}$
0.0−0.20
0.20−0.40
0.40−0.60
0.60−0.80
>0.80
Core forest (2km)
Edge forest (250m)
Homestead density (250m)
Structure density (1km)
Predictor Variable (β)

Figure 1-6



$P_{\neq 0}$
0.0–0.20
0.20–0.40
0.40–0.60
0.60–0.80
>0.80
1970's
2000's
Change
Cavity
Ground
Interior
Neotropical
Resident
Short Distance
Synanthrope
Core forest (2km)
Edge forest (250m)
Homestead density (250m)
Homestead×Edge
Structure density (1km)
Estimated Value of β (EV)
Predictor Variable (β)

Figure 1-7

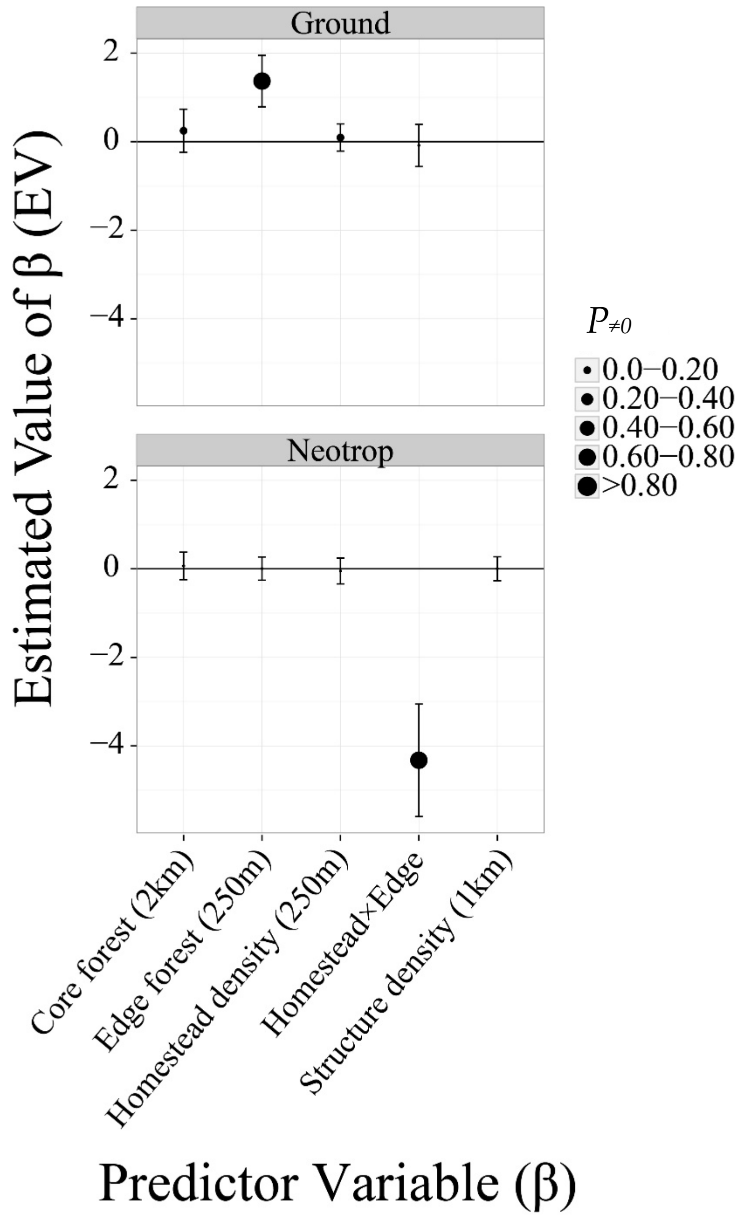

Ground
Neotrop
2
0
−2
−4
Estimated Value of β (EV)
P≠0
0.0−0.20
0.20−0.40
0.40−0.60
0.60−0.80
>0.80
Core forest (2km)
Edge forest (250m)
Homestead density (250m)
Homestead×Edge
Structure density (1km)
Predictor Variable (β)

Figure 1-8

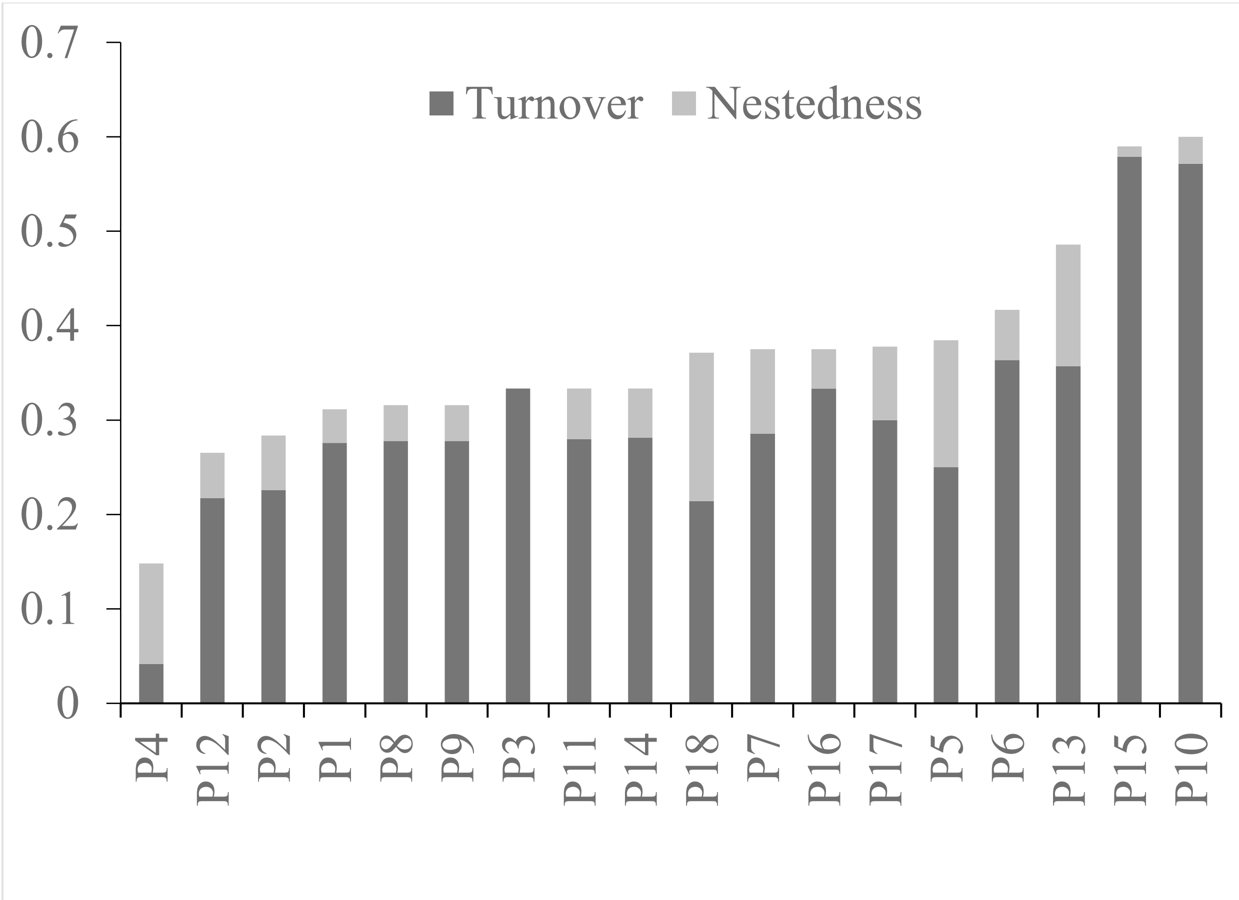
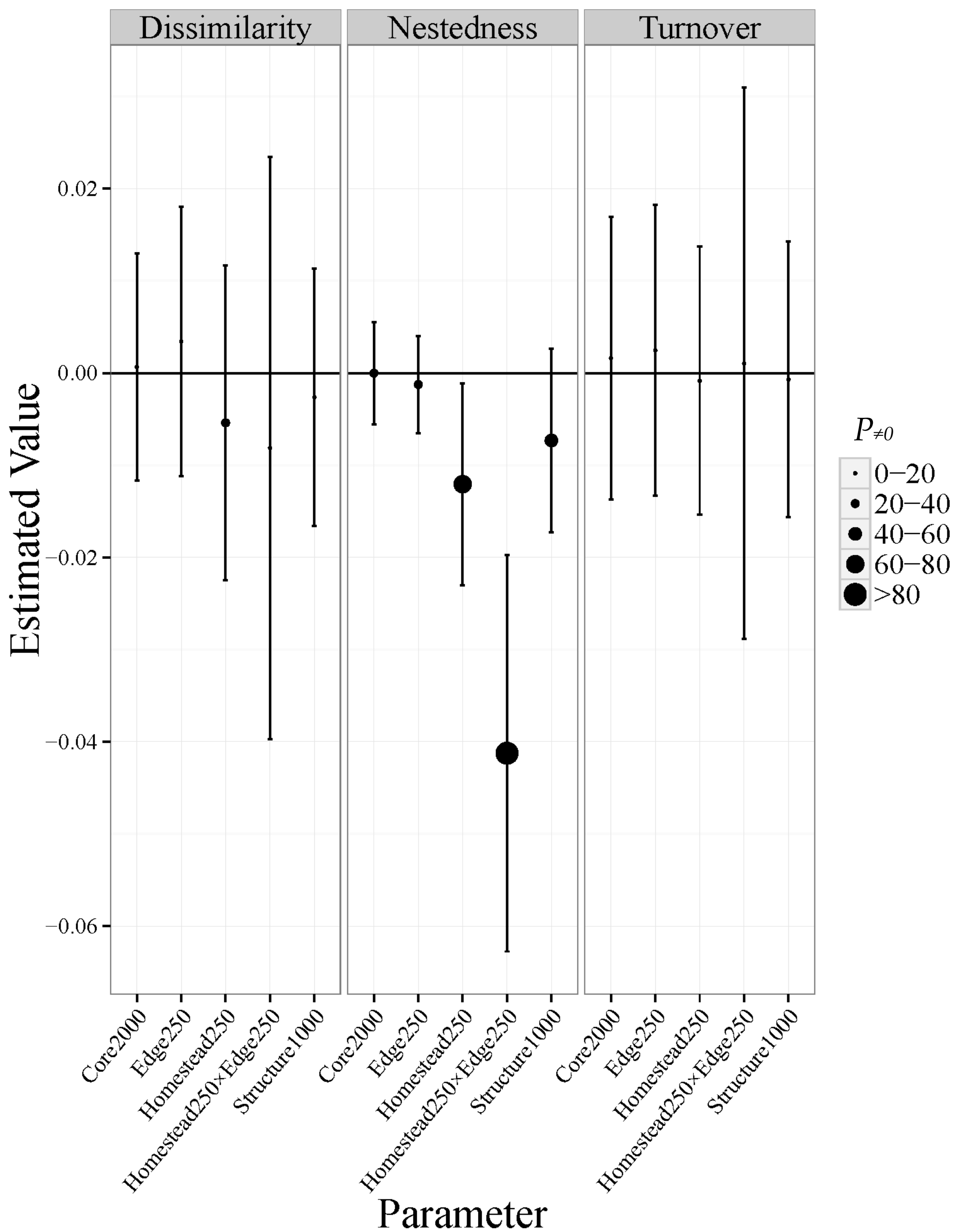

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Turnover
Nestedness
P4
P12
P2
P1
P8
P9
P3
P11
P14
P18
P7
P16
P17
P5
P6
P13
P15
P10

Figure 1-9



Dissimilarity
Nestedness
Turnover
Estimated Value
0.02
0.00
−0.02
−0.04
−0.06
Core2000
Edge250
Homestead250
Homestead250×Edge250
Structure1000
Parameter
$P_{\neq 0}$
0−20
20−40
40−60
60−80
>80

Figure 1-10

1-9 Appendices

Appendix 1-1 Table of the common names of birds identified within the study area, their associated four-letter AOU code, and guild memberships.

Appendix 1-2 Univariate plots of the relationship between the plot-level change in the relative abundance of Neotropical migrants and the change in (a) homestead density within 250m of a transect, (b) edge forest cover within 250m of a transect, and (c) the interaction between homestead density within 250m of a transect and edge forest cover within 250m of a transect.

Appendix 1-3 Results from Bayesian model averaging of the relationship between the relative abundance of birds within guilds (columns) and land cover and rural development within and between sampling periods (rows). Circles represent the probability a predictor variable does not equal zero ($p(\neq 0)$). Error bars represent one standard deviation of the estimated value for the predictor.

Appendix 1-4 Species relative abundance, defined as abundance divided by total bird abundance, within each sampling period, as well as the change in species' relative abundance between sampling periods within each study plot.

Appendix 1-1

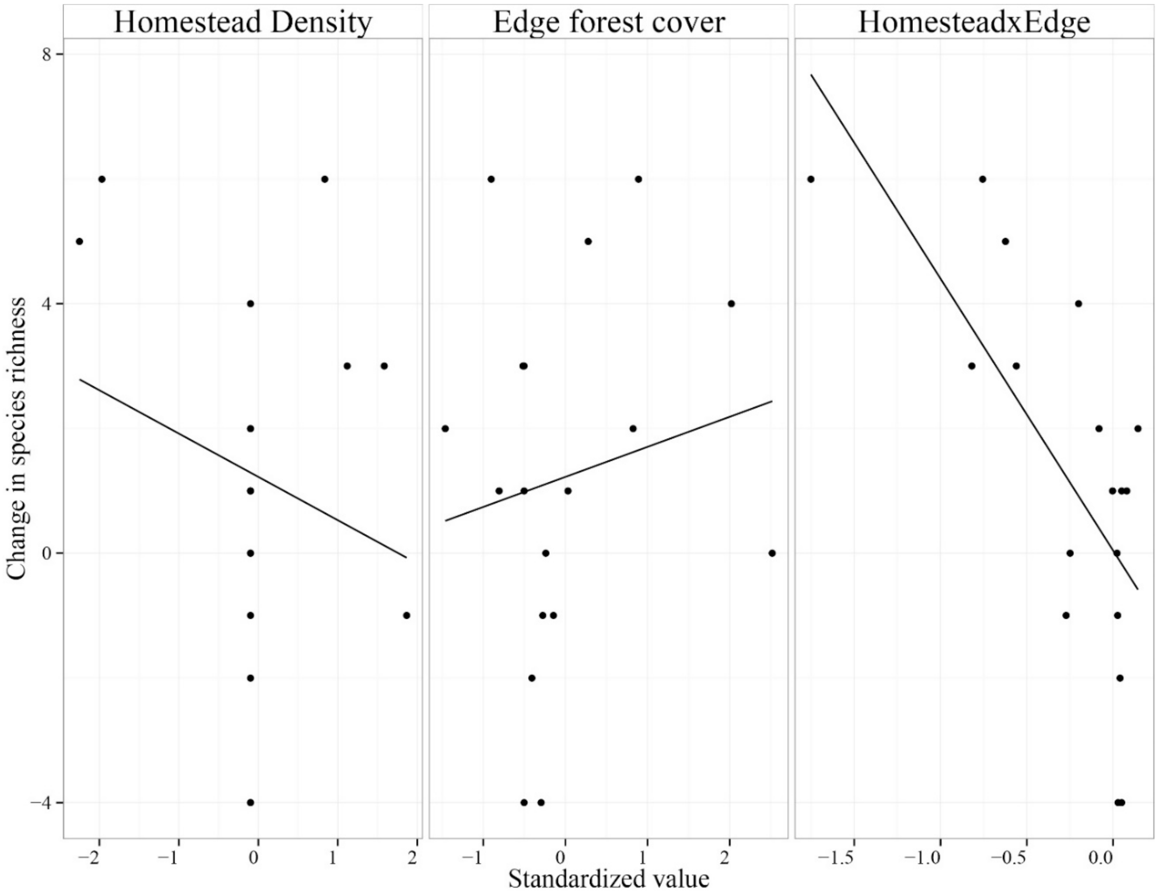
AOU code	Common name	Scientific name	Resident	Short distance migrant	Neotropical migrant	Interior forest nesting	Cavity nesting	Ground nesting	Synanthrope
ACFL	Acadian Flycatcher	*Empidonax virescens*	--	--	X	X	--	--	--
ALFL	Alder Flycatcher	*Empidonax alnorum*	--	--	X	--	--	--	--
AMCR	American Crow	*Corvus brachyrhynchos*	--	X	--	--	--	--	--
AMGO	American Goldfinch	*Spinus tristis*	--	X	X	--	--	--	--
AMRE	American Redstart	*Setophaga ruticilla*	--	--	X	X	--	--	--
AMRO	American Robin	*Turdus migratorius*	--	X	--	--	--	--	X
AMWO	American Woodcock	*Scolopax minor*	--	--	--	--	--	X	--
BADO	Barred Owl	*Strix varia*	X	--	--	--	X	--	--
BAOR	Baltimore Oriole	*Icterus galbula*	--	--	X	--	--	--	--
BAWW	Black-and-white Warbler	*Mniotilta varia*	--	--	X	--	--	X	--
BCCH	Black-capped Chickadee	*Poecile atricapillus*	X	--	--	--	X	--	--
BEKI	Belted Kingfisher	*Megaceryle alcyon*	--	--	--	--	X	--	--
BGGN	Blue-gray Gnatcatcher	*Polioptila caerulea*	--	--	X	--	--	--	--
BHCO	Brown-headed Cowbird	*Molothrus ater*	--	X	--	--	--	--	--
BLJA	Blue Jay	*Cyanocitta cristata*	--	X	--	--	--	--	X
BLBW	Blackburnian Warbler	*Setophaga fusca*	--	--	X	X	--	--	--
BRCR	Brown Creeper	*Certhia americana*	--	X	--	--	X	--	--
BRTH	Brown Thrasher	*Toxostoma rufum*	--	X	--	--	--	--	--
BTNW	Black-throated Green Warbler	*Setophaga virens*	--	--	X	--	--	--	--
BWHA	Broad-winged Hawk	*Buteo platypterus*	--	--	X	X	--	--	--

AOU code	Common name	Scientific name	Resident	Short distance migrant	Neotropical migrant	Interior forest nesting	Cavity nesting	Ground nesting	Synanthrope
BWWA	Blue-winged Warbler	*Vermivora cyanoptera*	--	--	X	--	--	X	--
CAWA	Canada Warbler	*Cardellina canadensis*	--	--	X	X	--	X	--
CERW	Cerulean Warbler	*Setophaga cerulea*	--	--	X	X	--	--	--
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	--	X	--	--	--	--	--
CHSP	Chipping Sparrow	*Spizella passerina*	--	--	X	--	--	--	X
COGR	Common Grackle	*Quiscalus quiscula*	--	X	--	--	--	--	X
COHA	Cooper's Hawk	*Accipiter cooperii*	--	X	--	--	--	--	--
COYE	Common Yellowthroat	*Geothlypis trichas*	--	--	X	--	--	--	--
CSWA	Chestnut-sided Warbler	*Setophaga pensylvanica*	--	--	X	--	--	X	--
DOWO	Downy Woodpecker	*Picoides pubescens*	X	--	--	--	X	--	--
EAKI	Eastern Kingbird	*Tyrannus*	--	--	X	--	--	--	--
EAPH	Eastern Phoebe	*Sayornis phoebe*	--	X	--	--	--	--	--
EATO	Eastern Towhee	*Pipilo erythrophthalmus*	--	--	--	--	--	X	--
EAWP	Eastern Wood-Pewee	*Contopus virens*	--	--	X	--	--	--	--
FISP	Field Sparrow	*Spizella pusilla*	--	X	--	--	--	--	--
GBHE	Great Blue Heron	*Ardea herodias*	--	X	--	--	--	--	--
GCFL	Great Crested Flycatcher	*Myiarchus crinitus*	--	--	X	--	X	--	--
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	--	X	--	--	--	--	--
GHOW	Great Horned Owl	*Bubo virginianus*	X	--	--	--	--	--	--
GRCA	Gray Catbird	*Dumetella carolinensis*	--	--	X	--	--	--	--
GWWA	Golden-winged Warbler	*Vermivora chrysoptera*	--	--	X	--	--	X	--

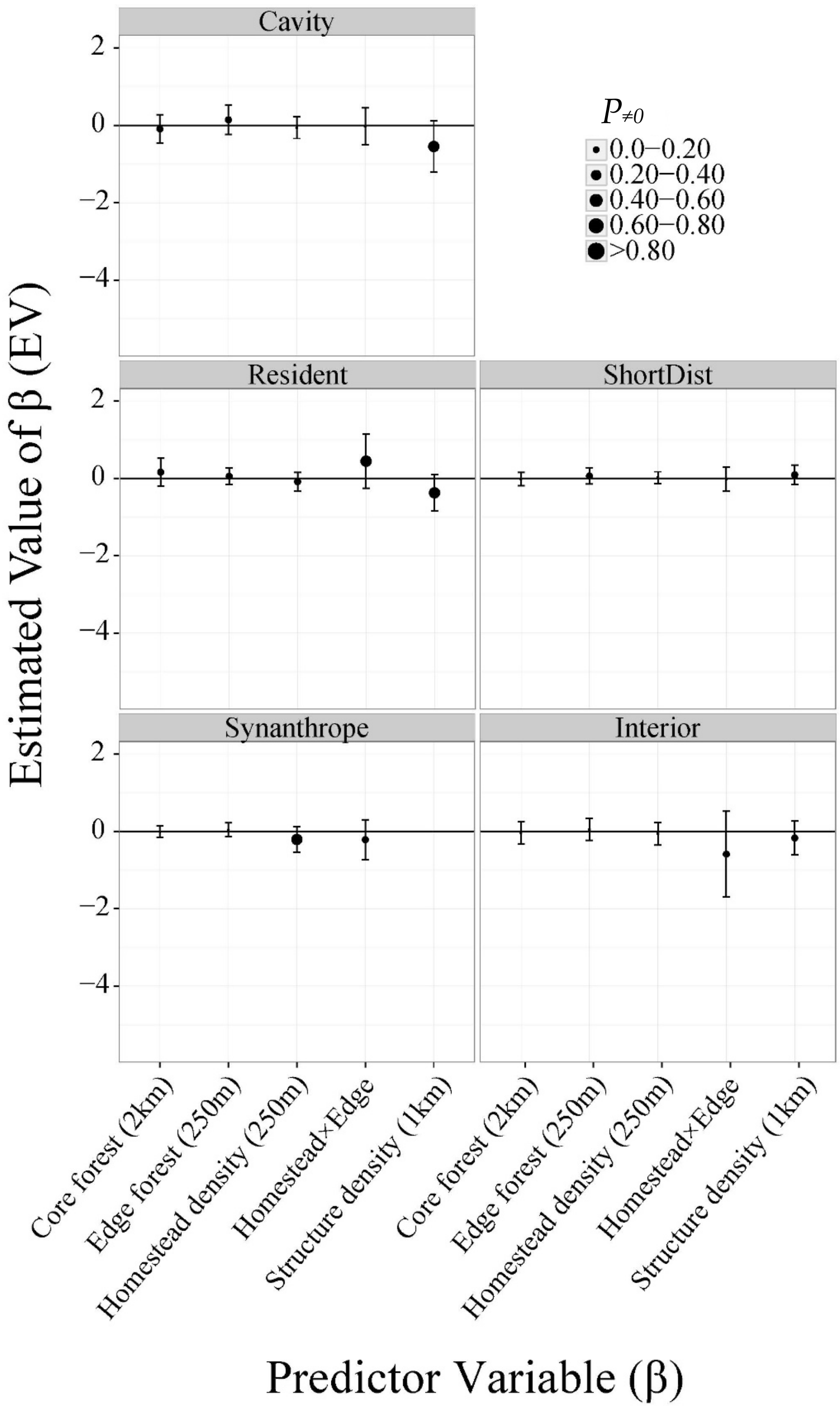
AOU code	Common name	Scientific name	Resident	Short distance migrant	Neotropical migrant	Interior forest nesting	Cavity nesting	Ground nesting	Synanthrope
HAWO	Hairy Woodpecker	*Picoides villosus*	X	--	--	--	X	--	--
HETH	Hermit Thrush	*Catharus guttatus*	--	X	--	X	--	X	--
HOWA	Hooded Warbler	*Setophaga citrina*	--	--	X	X	--	--	--
HOWR	House Wren	*Troglodytes aedon*	--	X	X	--	X	--	X
INBU	Indigo Bunting	*Passerina cyanea*	--	--	X	--	--	--	--
LEFL	Least Flycatcher	*Empidonax minimus*	--	--	X	--	--	--	--
LOWA	Louisiana Waterthrush	*Parkesia motacilla*	--	--	X	--	--	X	--
AMKE	American Kestrel	*Falco sparverius*	--	X	--	--	X	--	--
MODO	Mourning Dove	*Zenaida macroura*	--	X	--	--	--	X	X
MOWA	Mourning Warbler	*Geothlypis philadelphia*	--	--	X	--	--	X	--
NAWA	Nashville Warbler	*Oreothlypis ruficapilla*	--	--	X	--	--	X	--
NOCA	Northern Cardinal	*Cardinalis cardinalis*	X	--	--	--	--	--	--
NOFL	Northern Flicker	*Colaptes auratus*	--	X	--	--	X	--	--
NRWS	Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	--	--	X	--	--	--	--
OVEN	Ovenbird	*Seiurus aurocapilla*	--	--	X	X	--	X	--
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	X	--	--	X	X	--	--
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	--	--	X	--	--	--	--
RBWO	Red-bellied Woodpecker	*Melanerpes carolinus*	X	--	--	--	X	--	--
REVI	Red-eyed Vireo	*Vireo olivaceus*	--	--	X	X	--	--	--
RHWO	Red-headed Woodpecker	*Melanerpes erythrocephalus*	--	X	--	--	X	--	--
ROPI	Rock Pigeon	*Columba livia*	X	--	--	--	--	--	X
RTHA	Red-tailed Hawk	*Buteo jamaicensis*	--	X	--	--	--	--	--

AOU code	Common name	Scientific name	Resident	Short distance migrant	Neotropical migrant	Interior forest nesting	Cavity nesting	Ground nesting	Synanthrope
RTHU	Ruby-throated Hummingbird	*Archilochus colubris*	--	--	X	--	--	--	--
RUGR	Ruffed Grouse	*Bonasa umbellus*	X	--	--	--	--	X	--
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	--	X	--	--	--	--	--
SCTA	Scarlet Tanager	*Piranga olivacea*	--	--	X	X	--	--	--
SOSP	Song Sparrow	*Melospiza melodia*	--	--	--	--	--	X	--
TUTI	Tufted Titmouse	*Baeolophus bicolor*	X	--	--	--	X	--	--
TUVU	Turkey Vulture	*Cathartes aura*	--	X	--	--	X	X	--
VEER	Veery	*Catharus fuscescens*	--	--	X	--	--	X	--
WAVI	Warbling Vireo	*Vireo gilvus*	--	--	X	--	--	--	--
WBNU	White-breasted Nuthatch	*Sitta carolinensis*	X	--	--	--	X	-- --	
WEWA	Worm-eating Warbler	*Helmitheros vermivorum*	--	--	X	X	--	X	--
WITU	Wild Turkey	*Meleagris gallopavo*	X	--	--	--	--	X	--
WIWR	Winter Wren	*Troglodytes hiemalis*	--	X	--	X	X	X	--
WODU	Wood Duck	*Aix sponsa*	--	--	X	--	X	X	--
WOTH	Wood Thrush	*Hylocichla mustelina*	--	--	X	X	--	--	--
YBCU	Yellow-billed Cuckoo	*Coccyzus americanus*	--	--	X	--	--	--	--
YTVI	Yellow-throated Vireo	*Vireo flavifrons*	--	--	X	--	--	--	--

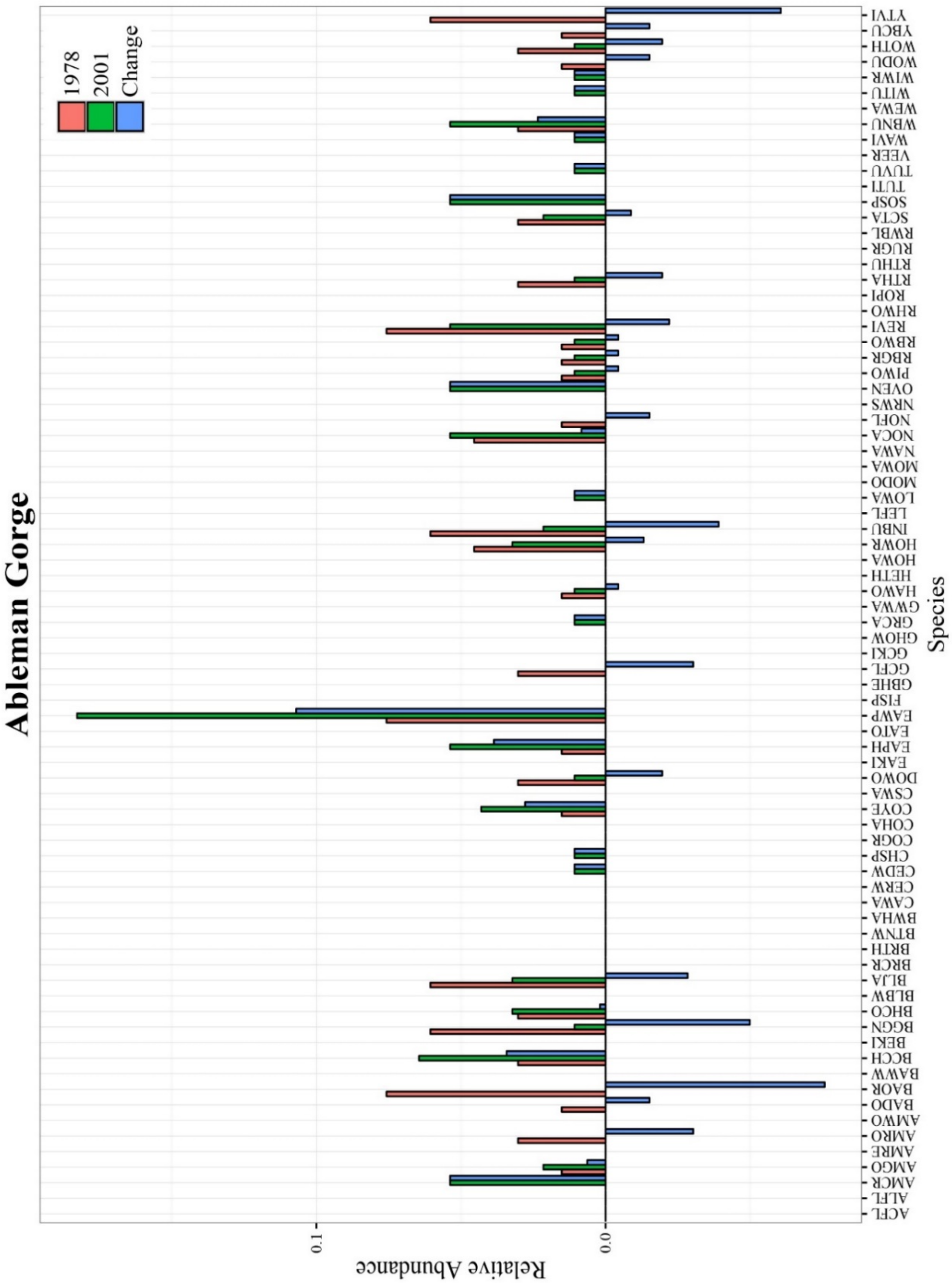
Appendix 1-2

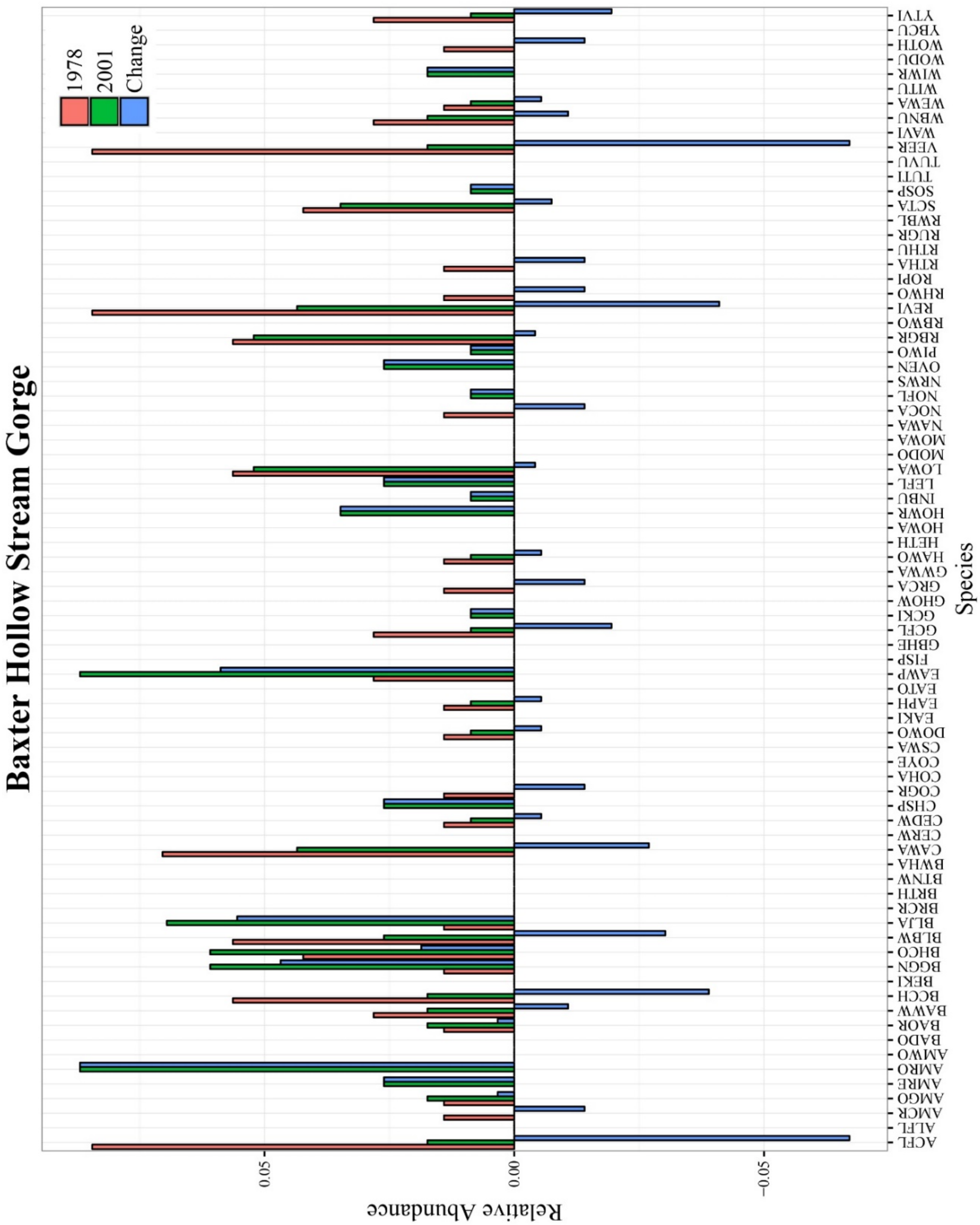

Homestead Density
Edge forest cover
HomesteadxEdge
Change in species richness
Standardized value
8
4
0
−4
−2
−1
0
1
2
−1
0
1
2
−1.5
−1.0
−0.5
0.0

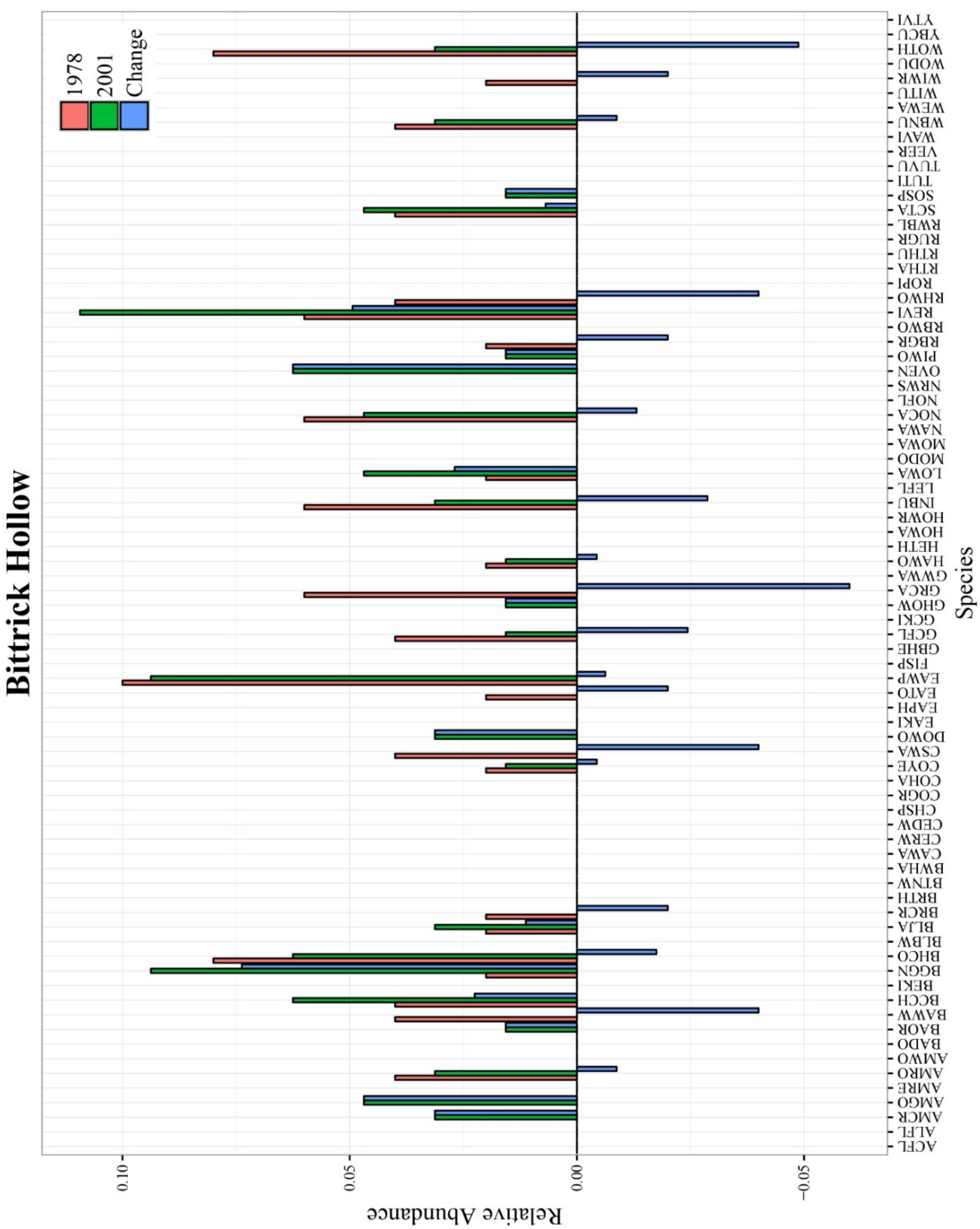
Appendix 1-3

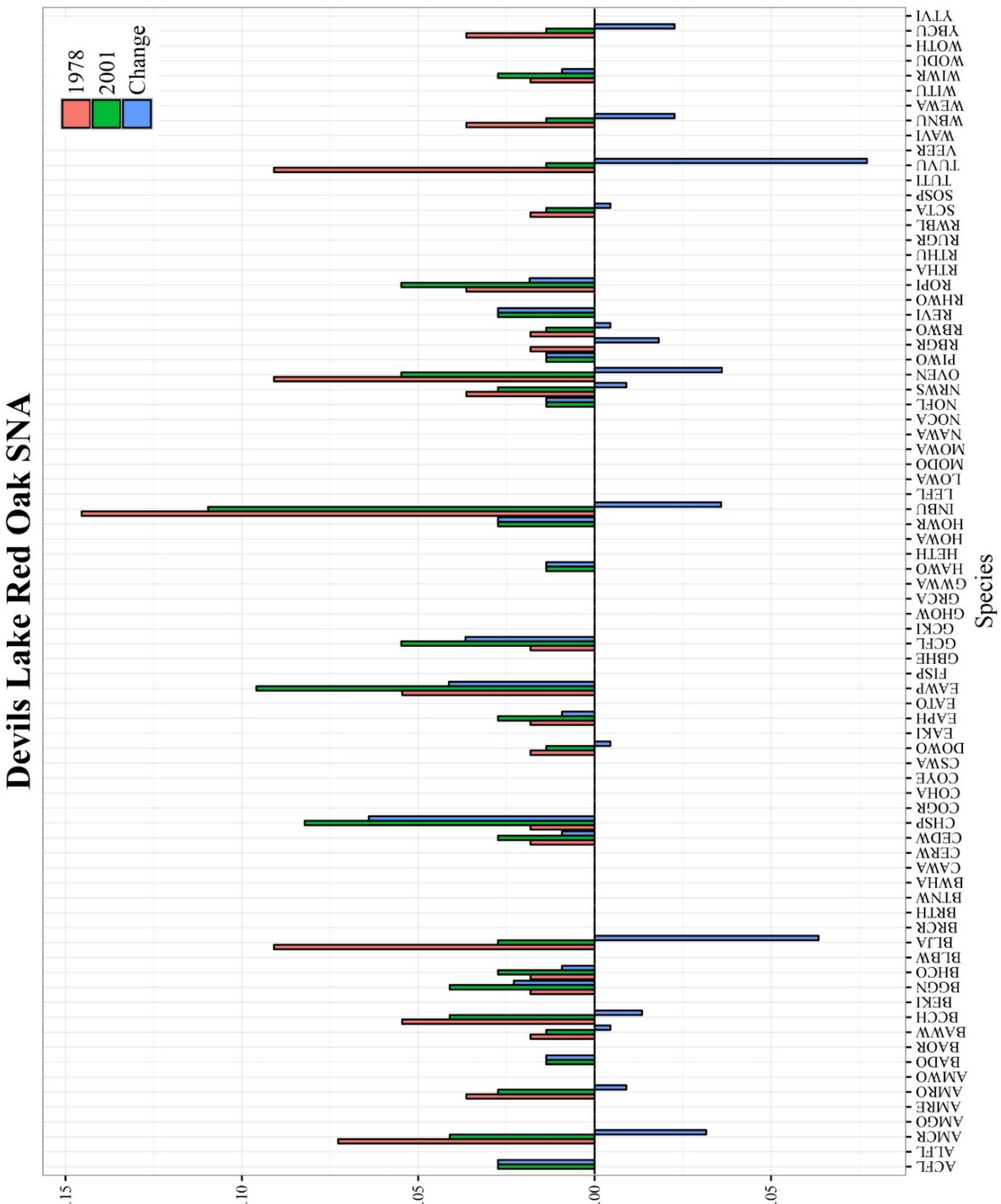

Cavity
Resident
ShortDist
Synanthrope
Interior
$P_{\neq 0}$
0.0−0.20
0.20−0.40
0.40−0.60
0.60−0.80
>0.80
Estimated Value of β (EV)
2
0
−2
−4
Core forest (2km)
Edge forest (250m)
Homestead density (250m)
Homestead×Edge
Structure density (1km)
Predictor Variable (β)

Appendix 1-4

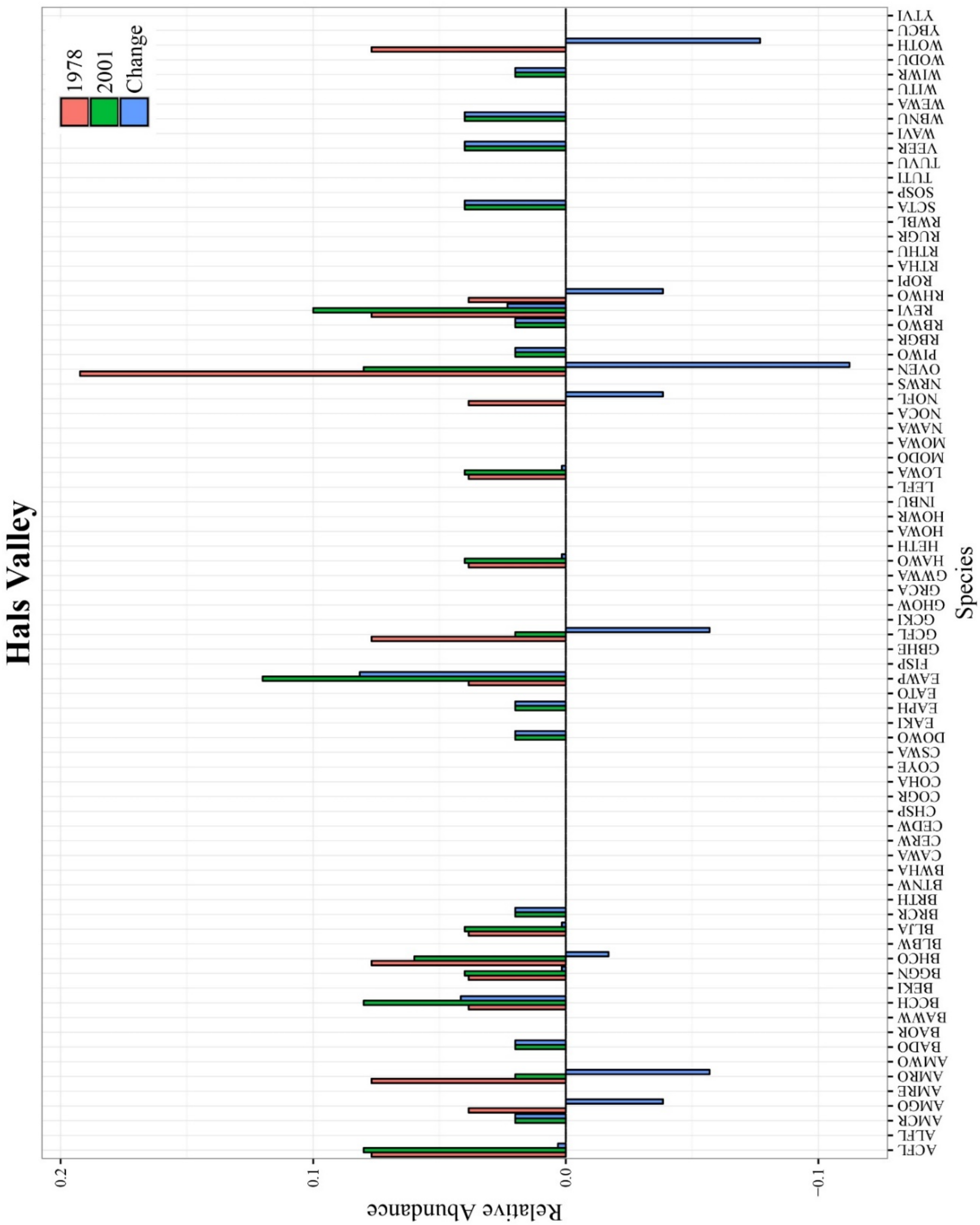

Ableman Gorge
1978
2001
Change
Species
Relative Abundance
0.0
0.1
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI

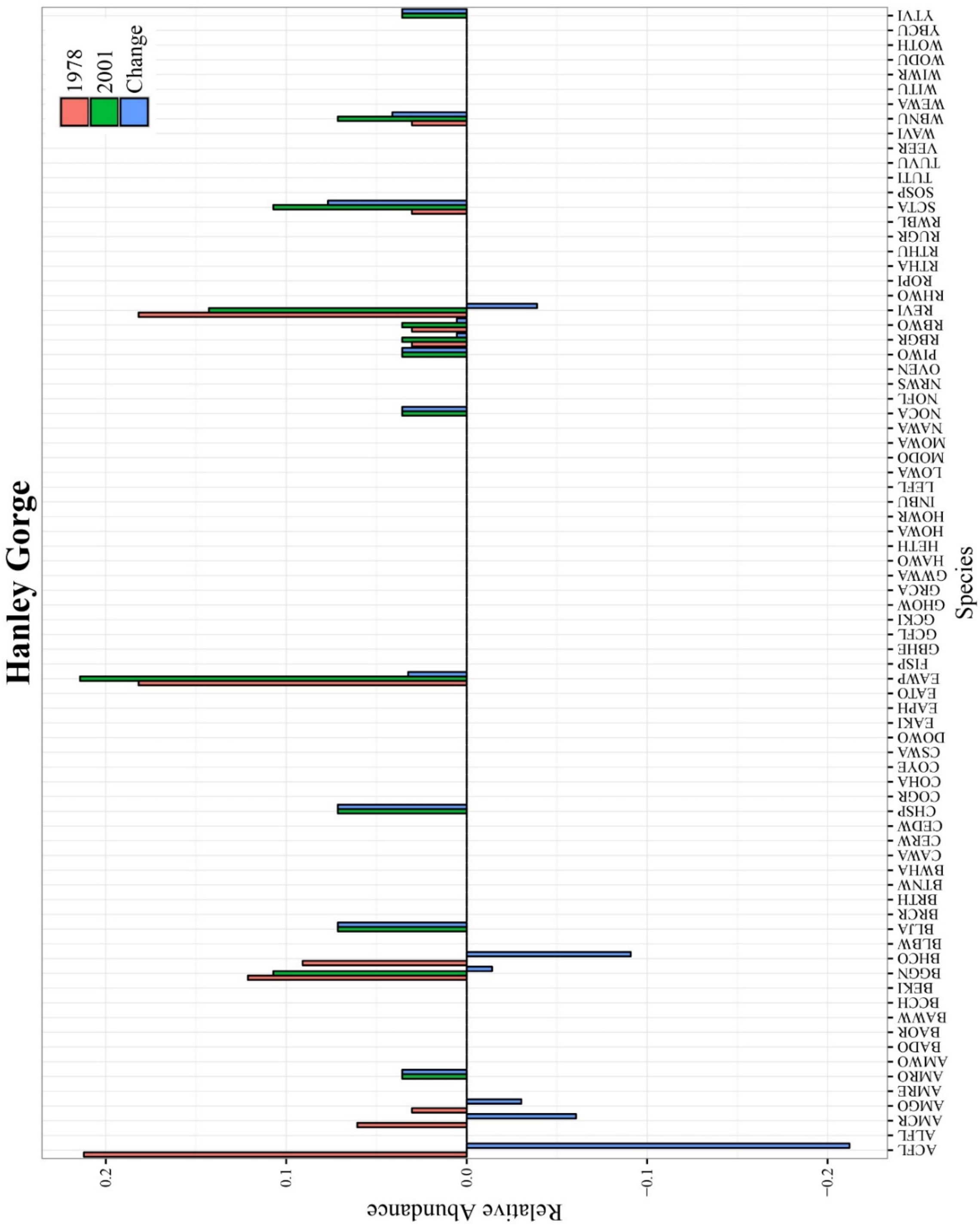

Baxter Hollow Stream Gorge
1978
2001
Change
Relative Abundance
0.05
0.00
−0.05
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI

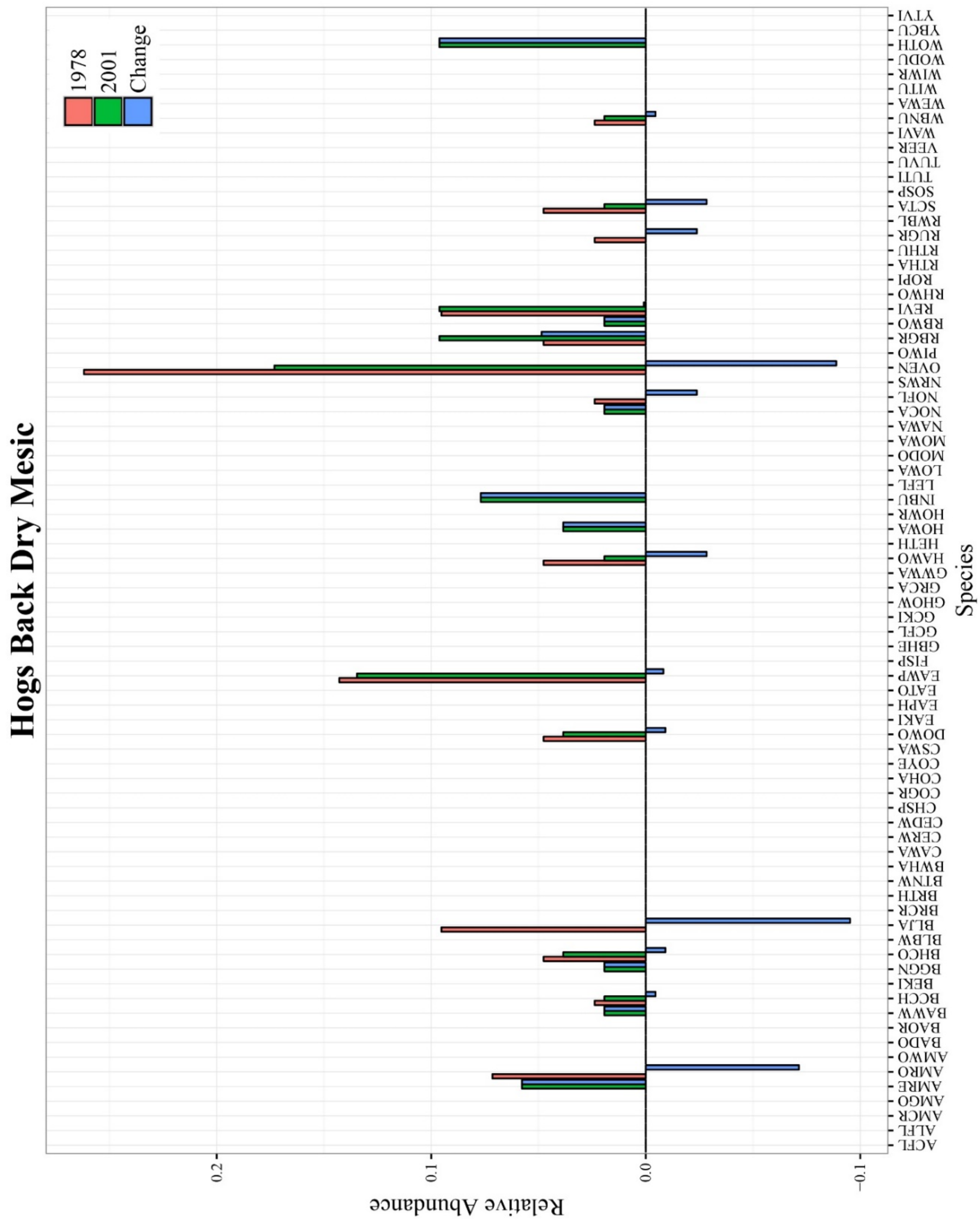

Bittrick Hollow
1978
2001
Change
Relative Abundance
0.10
0.05
0.00
−0.05
Species
ACFL ALFL AMCR AMGO AMRE AMRO AMWO BADO BAOR BAWW BCCH BEKI BGGN BHCO BLBW BLJA BRCR BRTH BTNW BWHA CAWA CERW CEDW CHSP COGR COHA COYE CSWA DOWO EAKI EAPH EATO EAWP FISP GBHE GCFL GCKI GHOW GRCA GWWA HAWO HETH HOWA HOWR INBU LEFL LOWA MODO MOWA NAWA NOCA NOFL NRWS OVEN PIWO RBGR RBWO REVI RHWO ROPI RTHA RTHU RUGR RWBL SCTA SOSP TUTI TUVU VEER WAVI WBNU WEWA WITU WIWR WODU WOTH YBCU YTVI



Devils Lake Red Oak SNA
Relative Abundance
0.15
0.10
0.05
0.00
−0.05
Species
1978
2001
Change
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Hals Valley
Relative Abundance
Species
1978
2001
Change
0.2
0.1
0.0
−0.1
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Hanley Gorge
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
−0.2
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Hogs Back Dry Mesic
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
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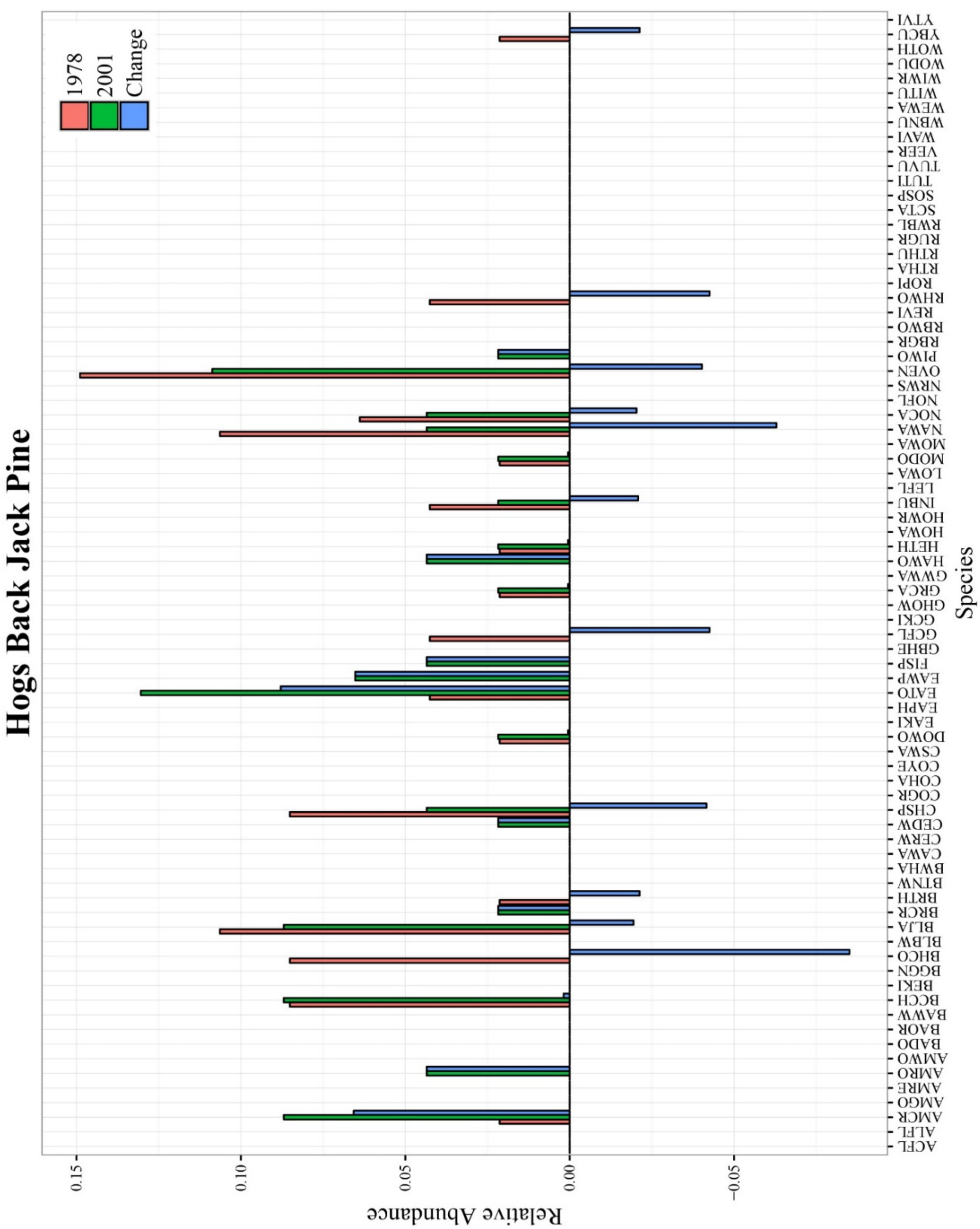
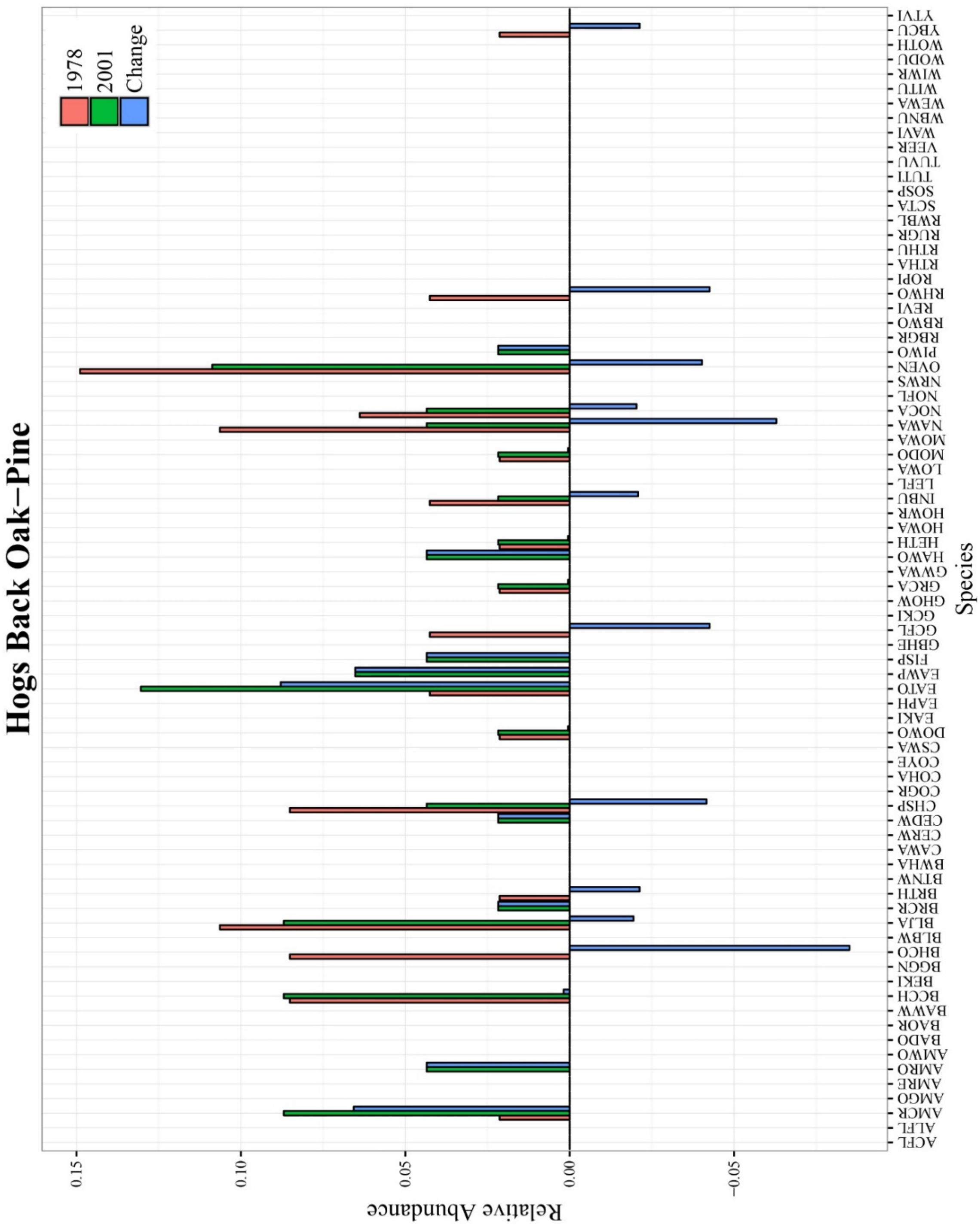
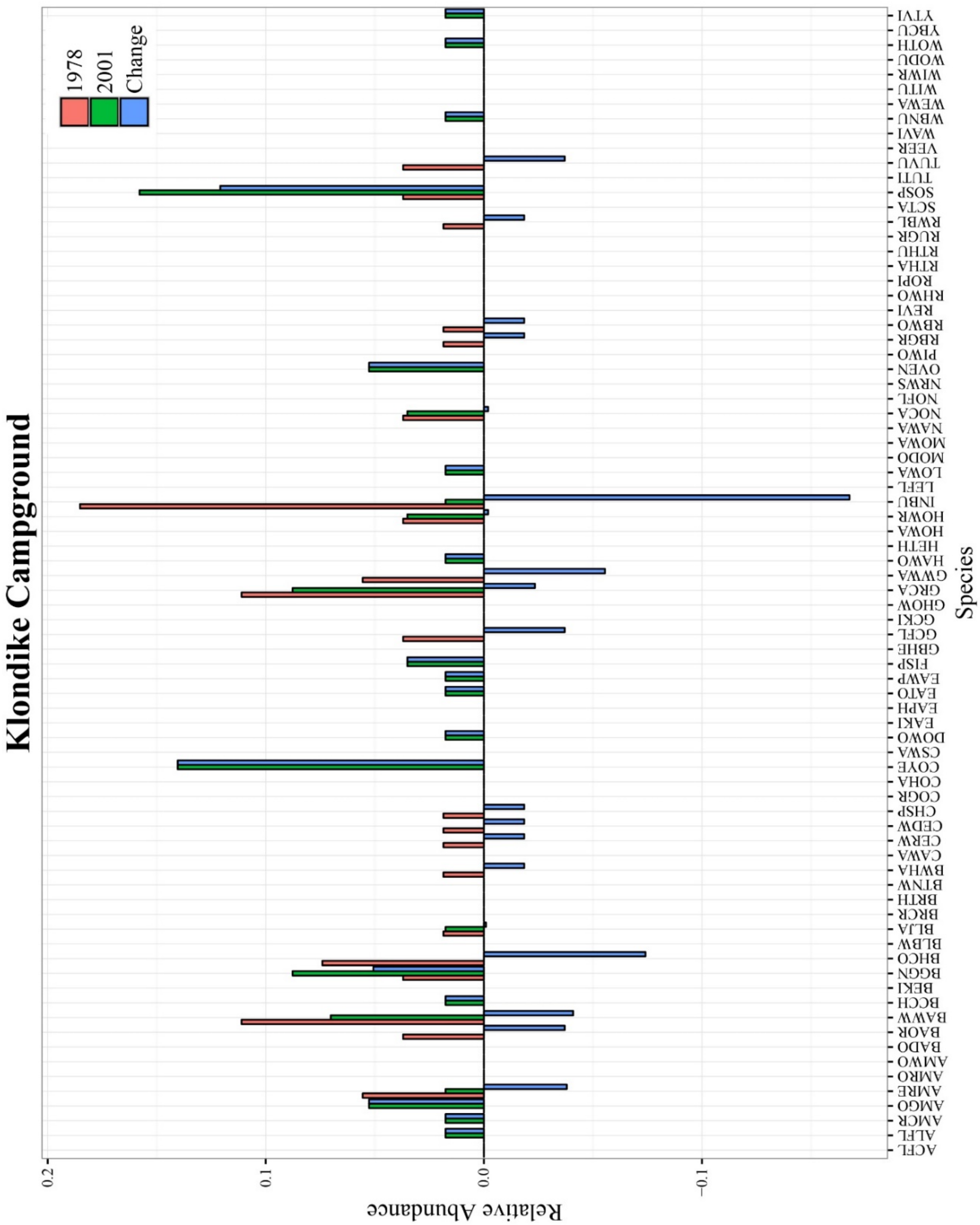
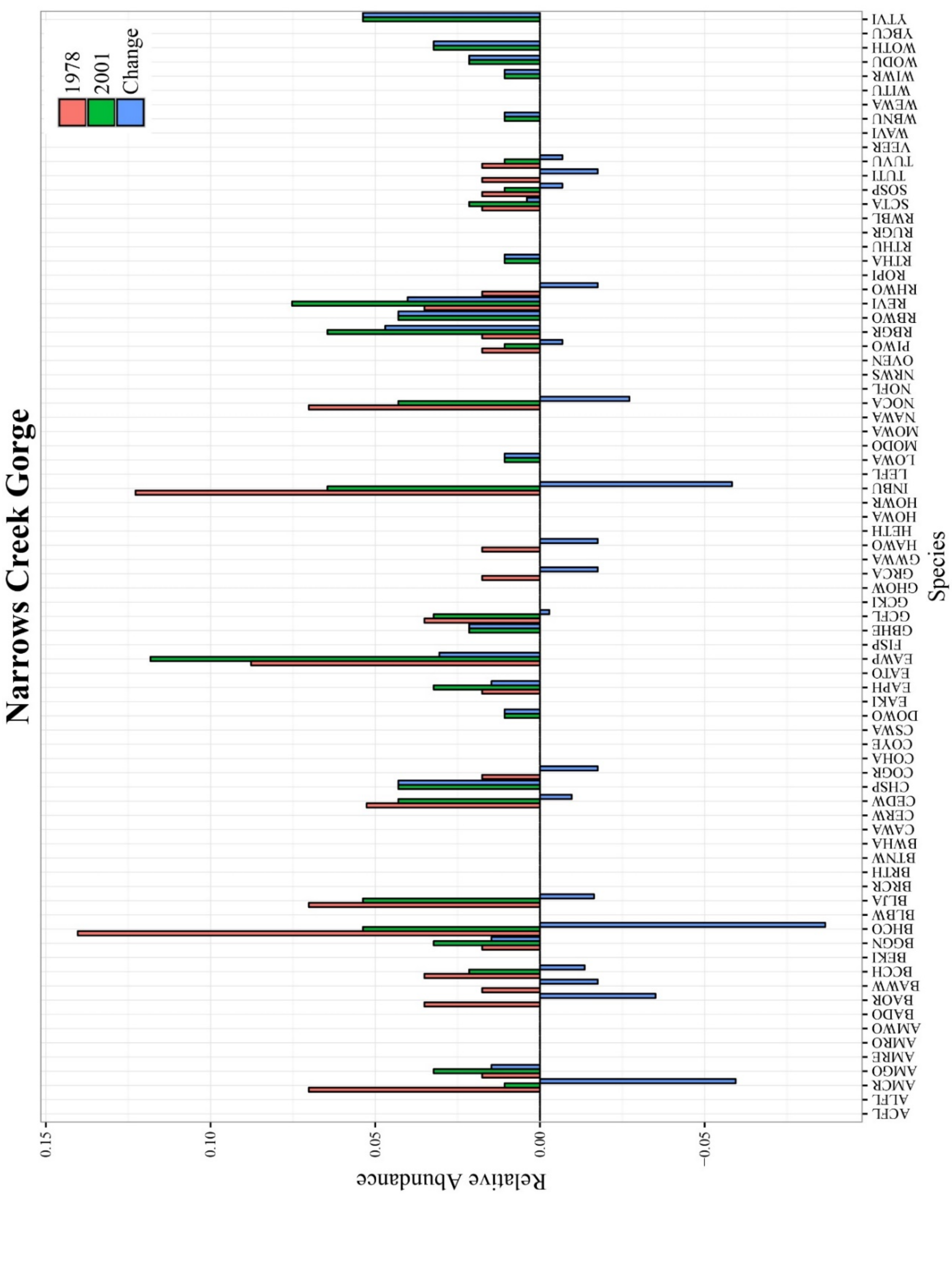
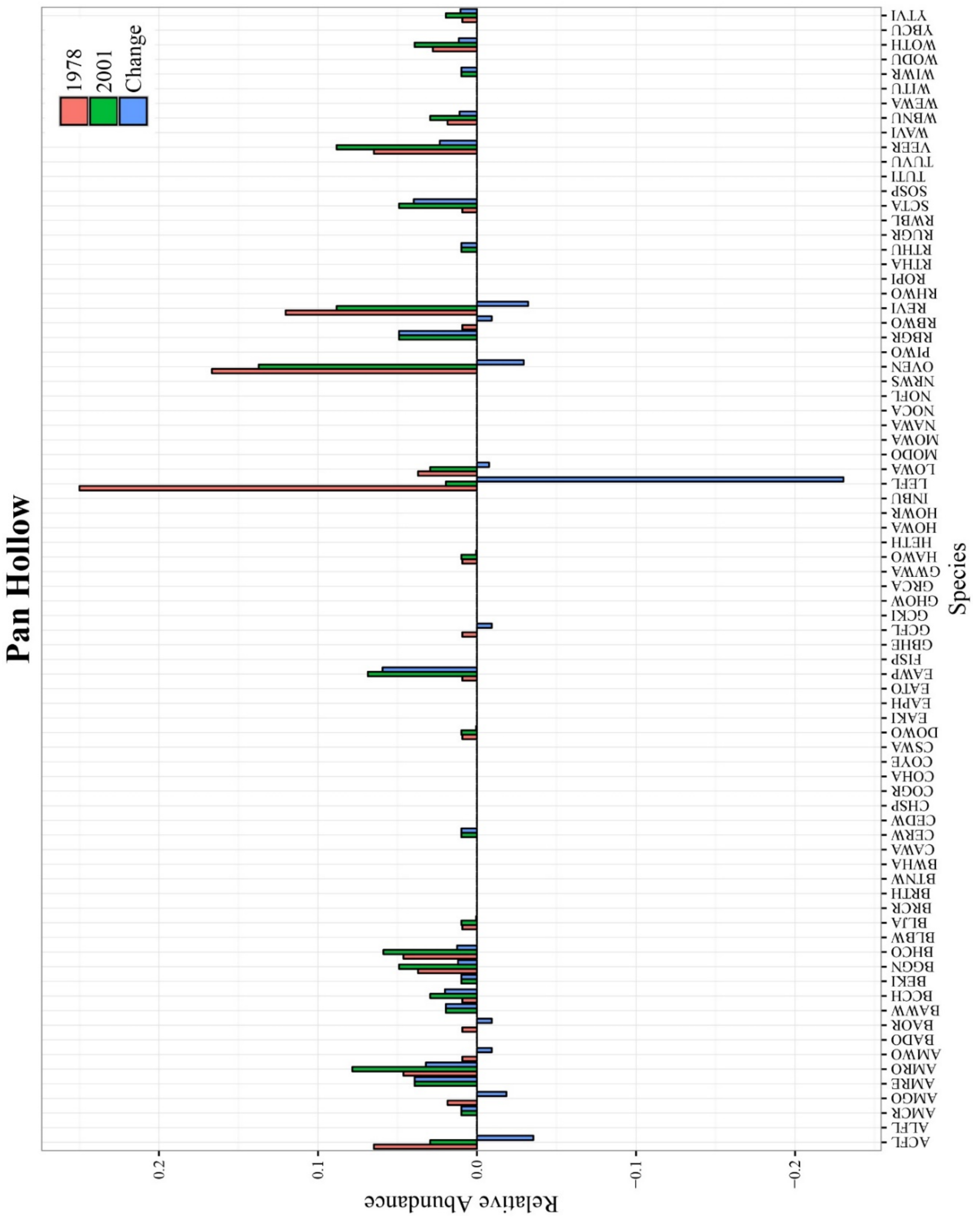
WIWR
WODU
WOTH
YBCU
YTVI


Hogs Back Jack Pine
1978
2001
Change
Relative Abundance
0.15
0.10
0.05
0.00
−0.05
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Hogs Back Oak−Pine
1978
2001
Change
Relative Abundance
0.15
0.10
0.05
0.00
−0.05
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Klondike Campground
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Narrows Creek Gorge
1978
2001
Change
Relative Abundance
0.15
0.10
0.05
0.00
−0.05
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI



Pan Hollow
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
−0.2
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
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TUVU
VEER
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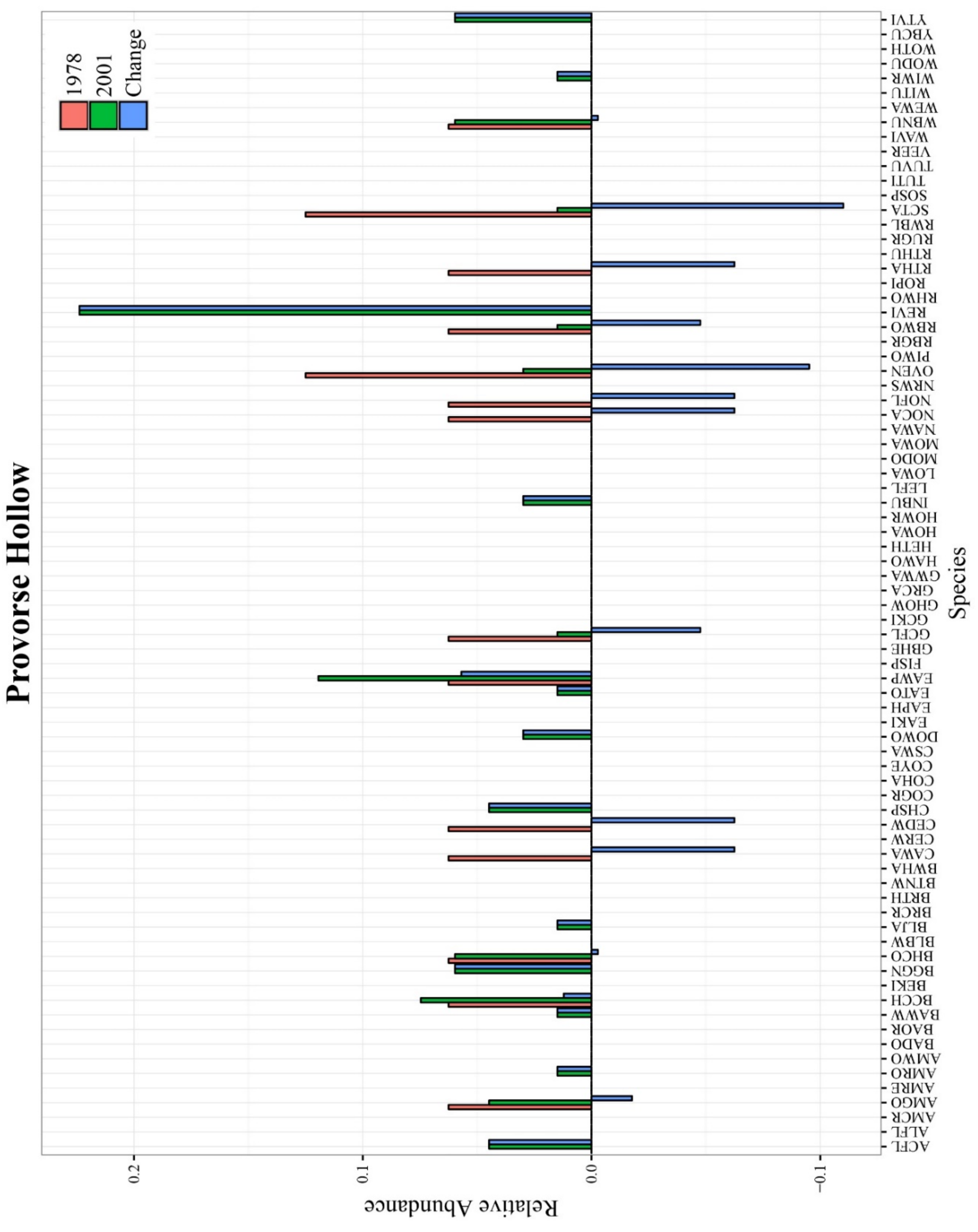
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Provorse Hollow
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
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WBNU
WEWA
WITU
WIWR
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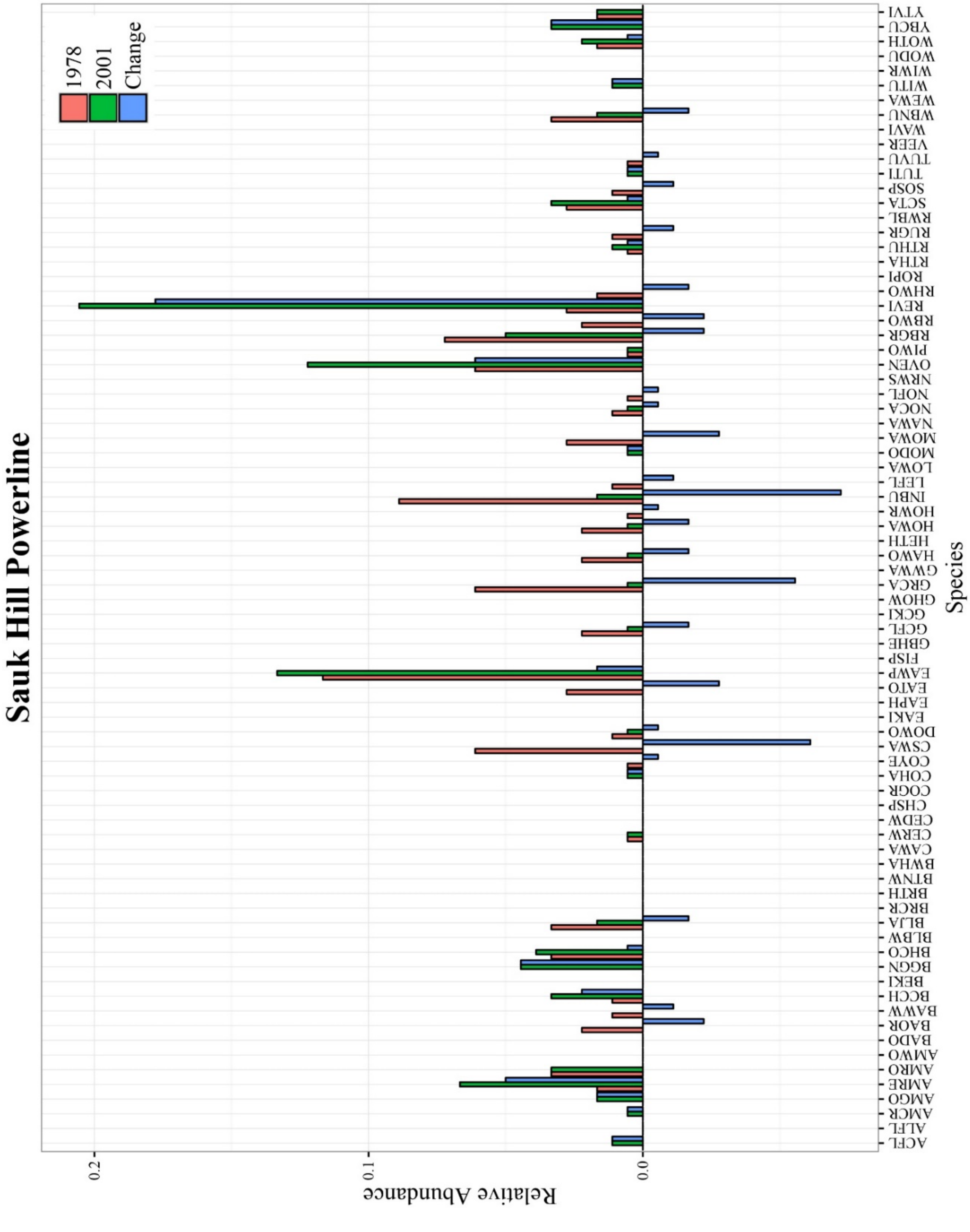
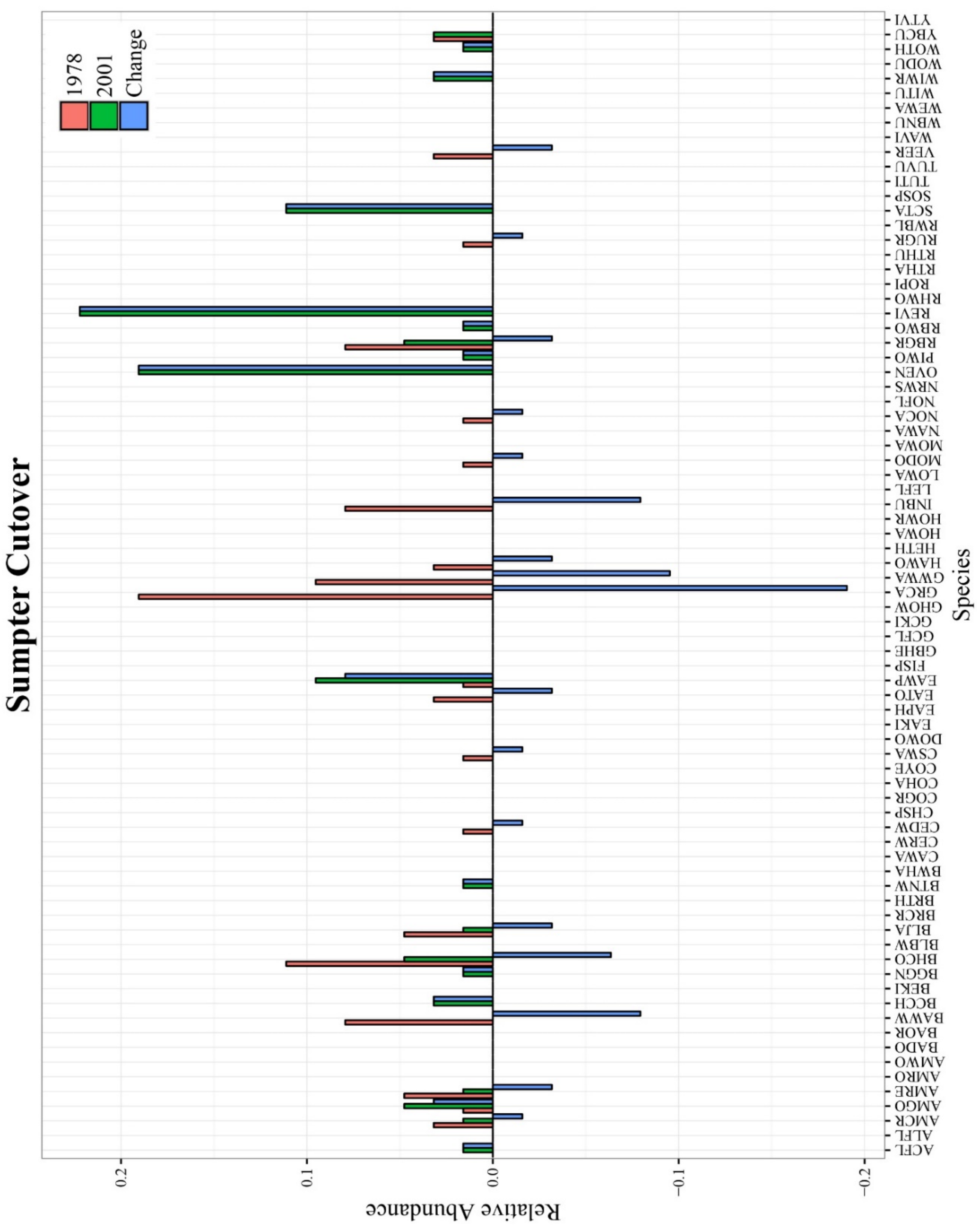
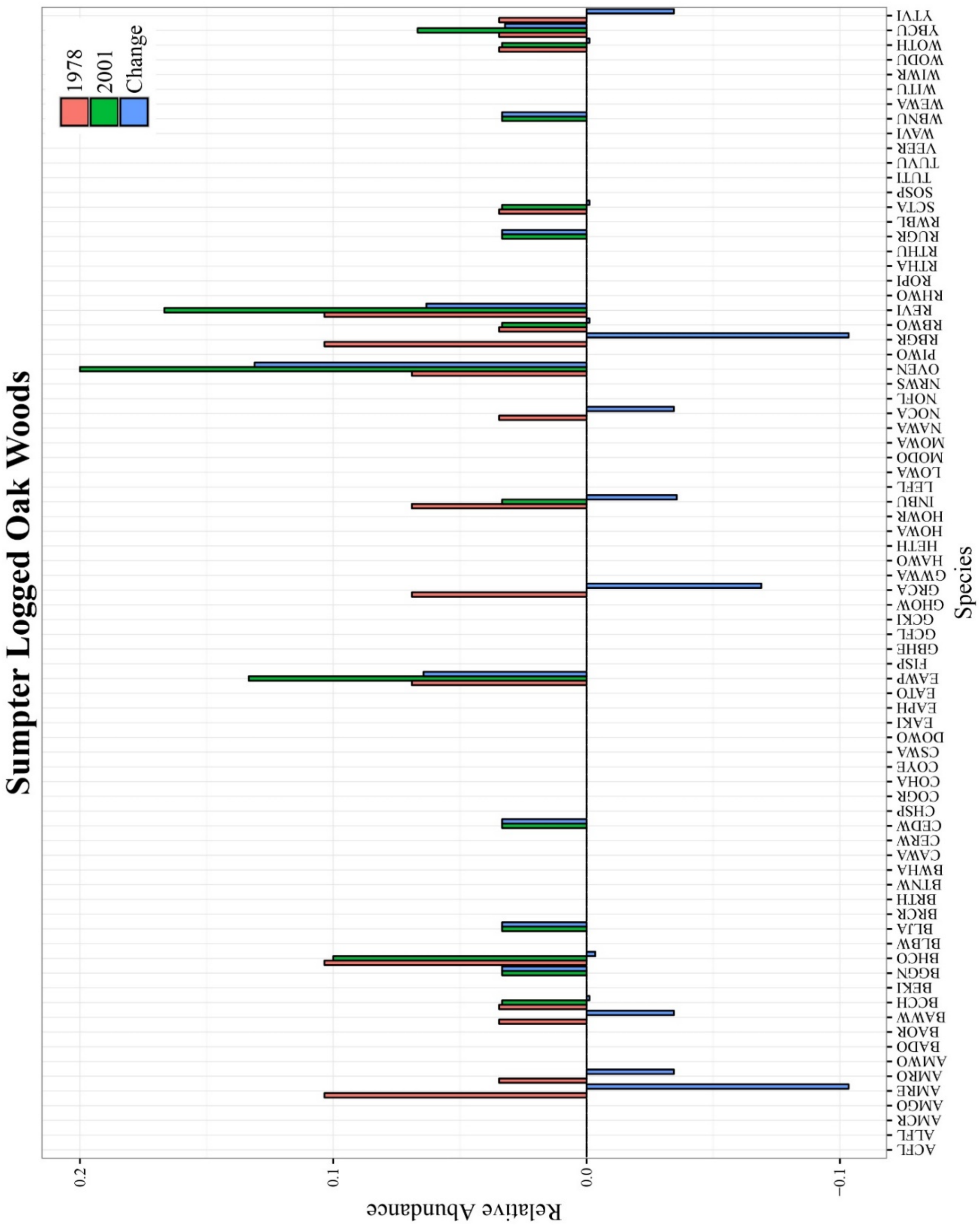
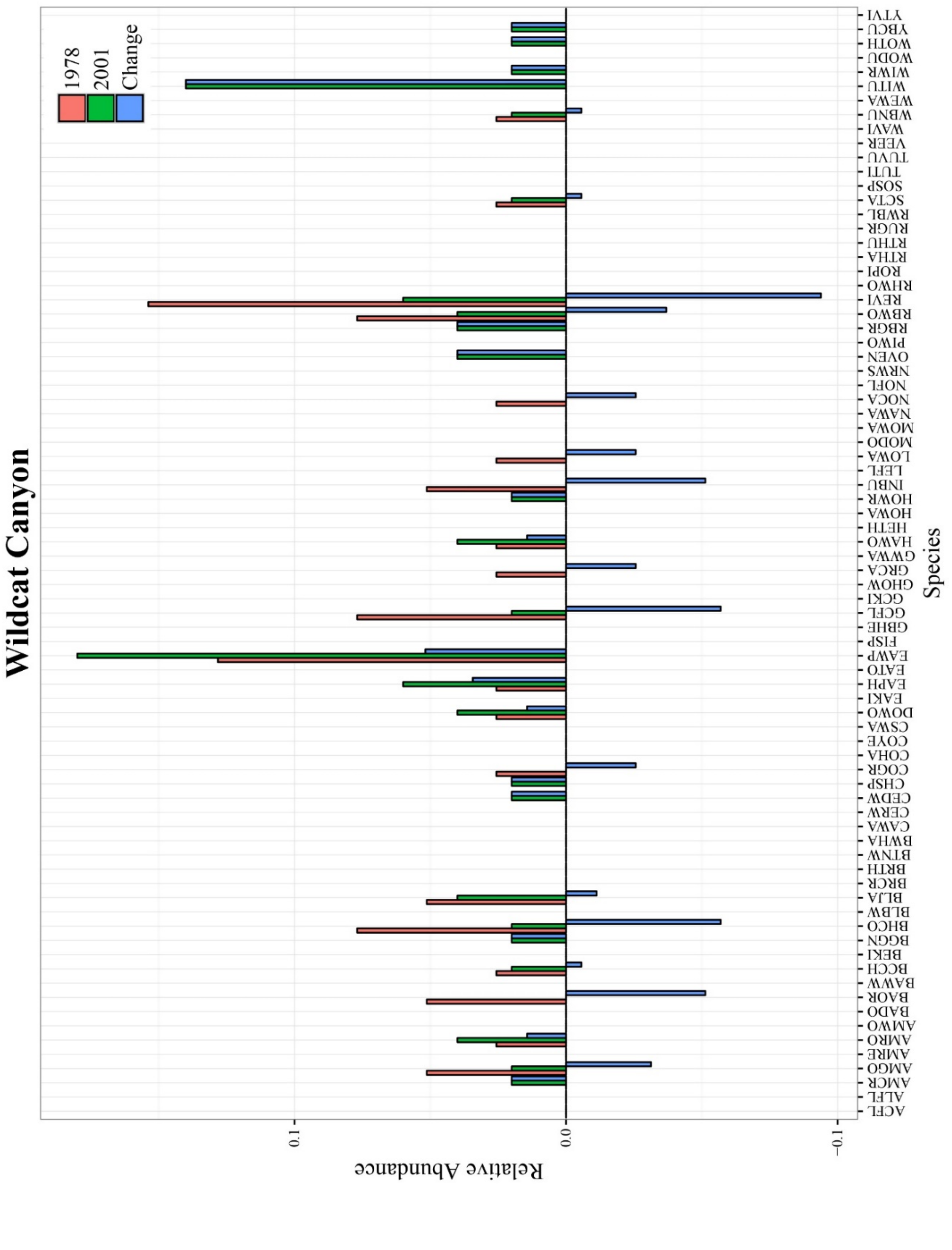
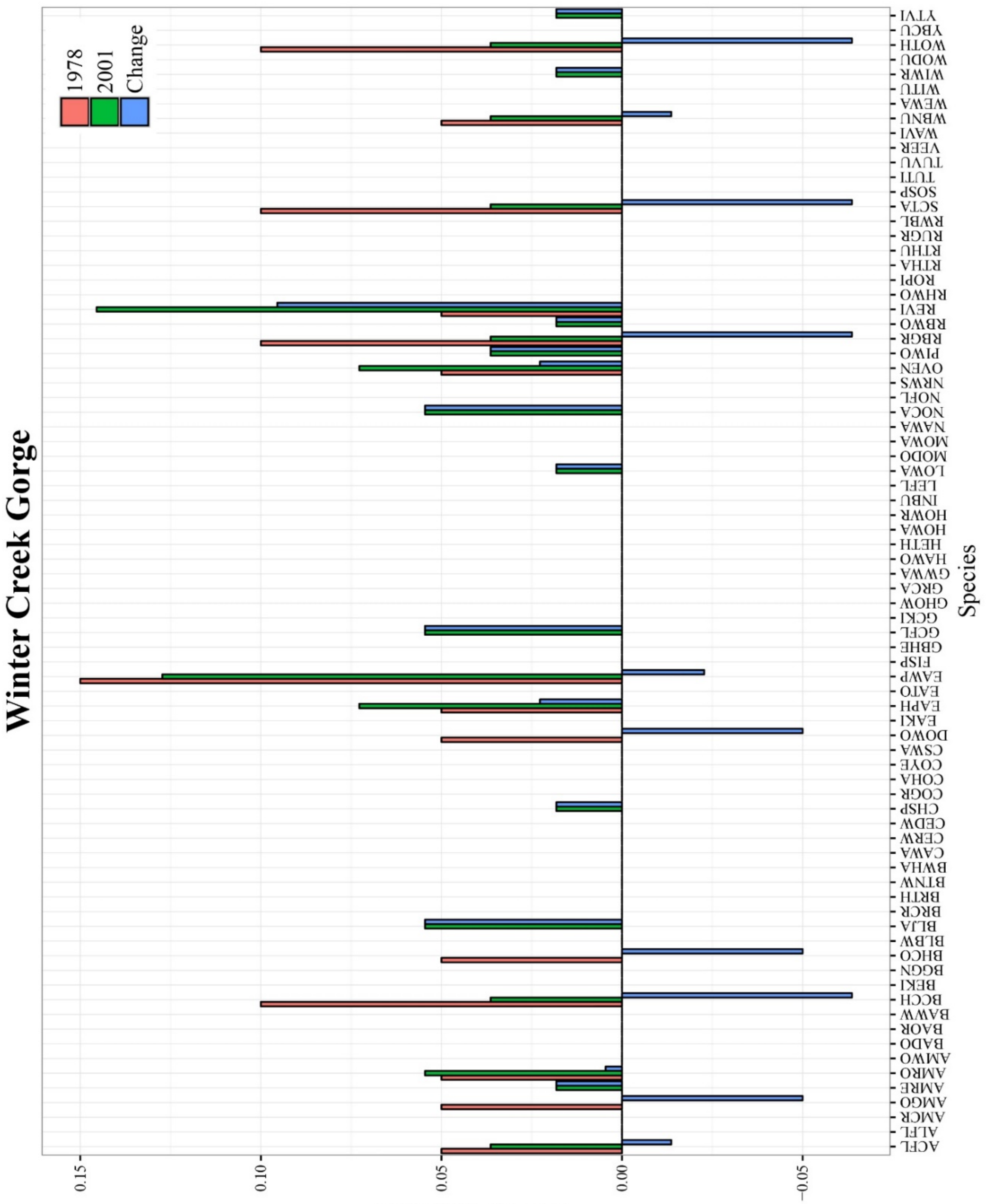
WOTH
YBCU
YTVI


Sauk Hill Powerline
1978
2001
Change
Relative Abundance
0.0
0.1
0.2
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Sumpter Cutover
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
−0.2
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Sumpter Logged Oak Woods
1978
2001
Change
Relative Abundance
0.2
0.1
0.0
−0.1
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Wildcat Canyon
1978
2001
Change
Species
Relative Abundance
0.1
0.0
−0.1
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI


Winter Creek Gorge
1978
2001
Change
Relative Abundance
0.15
0.10
0.05
0.00
−0.05
Species
ACFL
ALFL
AMCR
AMGO
AMRE
AMRO
AMWO
BADO
BAOR
BAWW
BCCH
BEKI
BGGN
BHCO
BLBW
BLJA
BRCR
BRTH
BTNW
BWHA
CAWA
CERW
CEDW
CHSP
COGR
COHA
COYE
CSWA
DOWO
EAKI
EAPH
EATO
EAWP
FISP
GBHE
GCFL
GCKI
GHOW
GRCA
GWWA
HAWO
HETH
HOWA
HOWR
INBU
LEFL
LOWA
MODO
MOWA
NAWA
NOCA
NOFL
NRWS
OVEN
PIWO
RBGR
RBWO
REVI
RHWO
ROPI
RTHA
RTHU
RUGR
RWBL
SCTA
SOSP
TUTI
TUVU
VEER
WAVI
WBNU
WEWA
WITU
WIWR
WODU
WOTH
YBCU
YTVI

Chapter 2: Recreational trails in protected areas alter avian community composition

2-1 Abstract

Increasing participation in outdoor recreation, particularly hiking, is considered a way to foster appreciation for nature and the environment. However, human use of forested protected areas may have unintended consequences due to both the presence of recreational trails and the presence of humans. Trails may alter forest structure by creating interior edge and associated increased vegetation volume, while the presence of humans may result in trail corridor avoidance by wildlife. Here, we examined whether the avian community in a forested region of southern Wisconsin differs in the vicinity of trails compared to areas without trails, and tested whether the trail, *per se*, or human use of trails alters avian community composition. Our objectives were to quantify bird community richness and individual bird species density, and to determine the relationship of these metrics with trail use, trail size, and habitat along trails. We found that community- and guild-level species richness was not strongly associated with trail use or characteristics. However, community composition was influenced by trail width and use. Birds affiliated with interior forest were found in greater density in study plots without trails than study plots with trails. The densities of nearly all forest species, but not non-forest species, was negatively associated with trail use and trail width. Our results suggest that trails in forests negatively affect native forest bird communities by creating unsuitable habitat along trail corridors which is related to trail width and trail use. We suggest that construction of new trails can minimize negative effects on declining songbird species by limiting vegetation removal and avoiding interior forest. Land managers who desire to both provide hiking opportunities and habitat for declining forest songbirds should carefully evaluate the importance of the wide trails on their properties, and consider revegetating the least important of these with native vegetation to reduce trail width.

Keywords: Recreation, birds

2-2 Introduction

Many of the world's protected areas serve the dual purpose of providing wildlife habitat and public hiking opportunities. The number of people hiking in protected areas has grown rapidly in recent decades, and threatens to undermine the goal of maintaining these areas as undisturbed habitat (Reed & Merenlender 2008). Trails serve as corridors for humans into otherwise mostly contiguous habitat in protected areas. Such access may have unintended consequences for bird communities by altering vegetation structure or creating areas avoided by species sensitive to human presence.

Forest hiking trails are typically constructed in one of two ways. Some trails are placed on former roads, such as those initially created for logging or fire control. These trails typically have a tread width, or area without vegetation, greater than 2 m and a broken or completely open canopy (Henschell et al, unpublished manuscript). The second method of trail construction is purpose-built. Purpose-built (or constructed) trails typically have a tread width of ~ 0.5 m, which limits the amount of vegetation removed, and thus maintains canopy conditions along the trail corridor that are similar to those in forest without trails (Tennessee Department of Environment and Conservation 2007).

Trails in forests, as relatively narrow corridors lacking vegetation, create a unique type of interior edge. The habitat discontinuity, though small, can alter the vegetation structure along the trail margins. If the trail is wide enough to result in a gap in the canopy, increased light transmittance along trails may result in increased foliage volume along the trail edge, similar to that found along roads and powerline corridors (Dale & Weaver 1974; Rich et al. 1994). Such changes to the vegetation structure in the forest interior may attract species not typically associated with interior forest conditions, such as Indigo Bunting (*Passerina cyanea*), which is typically associated with habitat edges (Hickman 1990).

Gill et al (2001) proposed two mechanisms by which human disturbance can displace bird species, altering bird community composition: 1. Species sensitive to human disturbance may avoid the disturbed area. Evidence in support of this mechanism would include an avian community near the disturbed area composed of a high proportion of species tolerant of the presence of humans (e.g. corvids, synanthropes) relative to undisturbed areas; 2. Habitat generalist species may settle in areas away from the disturbed area, while habitat specialists (e.g. interior forest birds) must settle in the area of the disturbance if there is no other suitable habitat available. Several studies investigating the effects of trails and trail use on birds lend support to the first hypothesis. For example, composition of the avian community was different along trails compared to undisturbed control areas in Finland, but total species richness did not differ between sites (Kangas et al. 2010). In Colorado, the abundance of several forest songbird species increased with distance from narrow trails (Miller et al. 1998), and in Peru conversational noise or other disruptive behavior by people using a trail resulted in fewer species being observed (Karp & Guevara 2011), which may have been due to displacement of some species from the trail corridor.

Here we tested whether the presence of a trail and the amount of trail foot traffic affected avian community composition in forested protected areas. We had four specific objectives. First, we investigated the effects of trails, trail use, and landscape and habitat characteristics near trails on species richness. We expected to see fewer interior forest nesting species and Neotropical migrant species as trail use increased, as we thought forest species would avoid human disturbance and/or altered habitat structure along trail edges. Second, we examined patterns of avian community composition along hiking trails. We predicted that bird communities would differ between old road trails and constructed trails/interior plots, primarily due to changes in habitat structure along old road trails. Third, we investigated patterns of bird species' density along trails. We expected that forest passerines would have lower density along wide, heavily used trails, due to changes in habitat along trails and avoidance of human disturbance.

2-3 Methods

2-3.1 STUDY AREA AND SAMPLING DESIGN

Our study area was the Baraboo Hills of southern Wisconsin (Figure 2-1). The Baraboo Hills are an area of ~58,000 ha, with ~22,000 ha of forested area. The forests are composed of southern hardwood species (e.g. white oak [*Quercus alba*], bitternut hickory [*Carya cordiformis*]), and northern hardwood forest species (e.g. eastern hemlock [*Tsuga canadensis],* and yellow birch [*Betula alleghaniensis*]) (Curtis 1959). The climate is humid continental, with large variations in seasonal temperatures (Peel et al. 2007).

The Baraboo Hills lie along the eastern boundary of the Wisconsin driftless area and have unique geologic formations including quartzite outcrops and the gorge of the Wisconsin River, known as the Dells of the Wisconsin River. The latter was important in the region becoming a major tourism destination. The region has several state parks, including Devil's Lake State Park, Wisconsin's most visited state park with over 1.5 million visitors/yr. Due to the unique geology and associated habitats of the region, approximately 50% of the forested area is protected, either by state or non-governmental organizations, such as The Nature Conservancy (US Geological Survey Gap Analysis Program (GAP) 2012), much of which is open to recreational access.

We established 27 plots in forested protected areas across the Baraboo Hills: nine plots were located in interior forests (interior plots) and the remaining 18 were located along trail segments in Wisconsin State Parks (SP), State Natural Areas (SNA), and The Nature Conservancy (TNC) and Wisconsin Society for Ornithology (WSO) preserves (figure 2-1). All plots were 500 m long by 100 m wide. Plots along trails were bisected along their length by the trail, while the interior plots were flagged along their length to indicate a "psuedo-trail." Plots were at least 250 m apart, and at least 100 m from any non-forested habitat. We classified plots along trails as "old roads" if the trail was located on a former road corridor, and as "constructed" if the trail was purpose-built as a recreational trail.

2-3.2 Quantifying avian communities

We established three point count stations in each plot to quantify the avian community. The point count stations were located equidistant along the trail or pseudo-trail within each plot. We recorded all bird species heard or seen within 75 m of each point count station during 10 minute surveys. We repeated the surveys 3 times during the breeding season (mid May–early July), separated by approximately 10 days, over three years, 2012–2014. We recorded wind speed, temperature, and sky condition at the beginning of each survey and surveyed only when the winds were less than 5 m/s, there was no heavy fog, and no rain

(Ralph et al. 1995). We began surveys at sunrise and continued for 3 hours, which permitted us to complete 6–9 points (2 or 3 plots) per day. All points within a plot were surveyed on the same day. Not all plots were surveyed within each survey period, primarily due to weather.

2-3.3 Habitat, trail, and landscape quantification

To quantify the habitat characteristics within each of our 27 plots, we located one 5 m radius vegetation survey at each point count station and randomly located six additional vegetation surveys throughout the plot (9 vegetation surveys in each plot). We counted all understory stems > 0.25 m high within the vegetation survey, and estimated understory stem density (Understory). We took hemispherical canopy photos at the center of each vegetation plot using a Nikon Coolpix 5000 camera with a Nikon Fisheye Converter FC-E8 lens. We took all of the photos at 1 m from the ground, and ensured that the plane of the sensor was level. We used ImageJ (Abràmoff et al. 2004) to calculate the canopy openness (OPEN) at each vegetation survey (A. Robertshaw, personal communication). We averaged vegetation values across the 9 surveys within each plot.

We measured foliage height diversity (FHD) at each vegetation survey using a 4 m tall PVC pole. We counted all vegetation touching the pole within 0.3 m increments. For vegetation above the pole, we estimated the number of vegetation layers intercepting the vertical line continuing up from the pole in 1.5 m increments (Wood et al 2012). We used the Shannon Diversity Index (H′) to calculate plot-level FHD.

We measured two widths of the recreational trail within each plot at each point count station. We measured the tread width (WTR) and the width clear of vegetation at 1.4 m from the ground (WBH), and averaged these measurements to obtain plot-level WTR and WBH values. We used passive infrared trail counters to quantify the average number of people per hour (GPH) using a trail during the breeding season (mid May–early July) in 2012-2014.

We created a binary forest/non-forest layer in ArcGIS (ESRI 2013) from the 2011 National Land Cover Database to quantify the land cover composition around trail plots (Homer et al. 2011). We included all NLCD "Forest" classes (41, 42, and 43) as forest land cover and all other classes as non-forest. We used this binary layer to determine core forest area within 5 km (Forest) and edge forest area within 500 m (Edge) of the plot center using morphological spatial pattern analysis (Vogt et al. 2007). We defined edge as any forest pixel within 60 m of a forest/non-forest boundary.

2-3.4 Statistical analysis

We assigned each species to a migration guild (resident, short distance, Neotropical), a nesting guild (forest interior, cavity, ground), and we identified the synanthrope guild based on Pidgeon et al (2007) and Peterjohn and Sauer (1993; Appendix 2-1). Guild memberships were not mutually exclusive. We calculated total species richness (S_{total}), interior forest-breeding species richness (S_{forest}), the richness of any species that is not primarily associated with forested ecosystems ($S_{non\text{-}forest}$), and Neotropical migrant species richness ($S_{neotropical}$).

We tested for differences among plot types in guild richness and in our explanatory variables (Understory, OPEN, FHD, WTR, WBH, Forest, and Edge) using analysis of variance, followed by Tukey's HSD Test with $\alpha = 0.05$ (Zar 2010). We investigated whether patterns in observed species richness were associated with trail width, trail use, habitat, or landscape variables using Bayesian model averaging (BMA). BMA provides improved predictive power by accounting for uncertainty in the model selection process (Raftery 1995; Hoeting et al. 2000). BMA is implemented using a BIC approximation where models included in the model average have ΔBIC < 6 and have no nested sub models with a lower BIC score (Raftery 1995). BMA output includes the estimate value (EV) for each model parameter, the standard deviation of each parameter estimate across all selected models (SD), and the posterior probability that the parameter estimate is not zero ($P_{\neq 0}$).

We used hierarchical open distance sampling models to account for imperfect detection and to estimate plot-level density (individuals/ha). Open distance sampling allows for modelling species density across multiple seasons by relaxing the assumption of closed populations (Dail & Madsen 2011). We used a stacked data structure, meaning that density was calculated for each point count station×year combination ($n = 81$). We considered observer, wind speed, start time of survey, and ordinal date as variables affecting detection in 11 candidate detection models (Appendix 2-2). We were able to fit models for 26 of 66 detected species. We used AIC to select the best detection model, which was then used in modelling plot-level density.

We used nonmetric multidimensional scaling (NMS) to investigate patterns of avian community composition among our three plot types and how community composition was associated with environmental variables. We used the plot-level rank Bray-Curtis dissimilarity matrix of the square-root transformed detection-only model density estimates of 26 species in the ordination (McCune et al. 2002). We used analysis of similarity with 999 Monte Carlo simulations to generate the ANOSIM R statistic (ANOSIM), testing whether community composition was different among plot types (Clarke 1993).

We considered 6 potential covariates (OPEN, Forest, Edge, WTR, WBH and GPH), and developed 31 *a priori* density models (Appendix 2-2), excluding highly correlated ($I > 0.70$; Table 2-1) explanatory variables from the same model (Tabachnick & Fidell 2012). We used model averaging to calculate parameter estimates for each species (Burnham & Anderson 2004). All analyses were completed in the R statistical environment, using the “vegan” package for multivariate methods and the “unmarked” package for open distance sampling (Fiske & Chandler 2011; Oksanen et al. 2013; R Core Development Team 2013).

2-4 Results

We found difference among plot types in tread width (WTR; $F_{2,24}$ = 71.99, P < 0.001), trail width at 1.4 m from the ground (WBH; $F_{2,24}$ = 108.30, P < 0.001), number of groups of trail users per hour (GPH; $F_{2,24}$ = 10.69, P < 0.001) and edge forest area within 500 m of the trail (Edge; $F_{2,24}$ = 3.65, P < 0.05; Table 2-2; Figure 2-2). WTR and WBH were different in all pair-wise comparisons (Tukey post-hoc test, P < 0.001 for all comparisons), while edge forest area was lower near interior plots than near old road plots (Tukey post-hoc test, P < 0.05; Table 2-2; Figure 2-2). GPH was not associated with the slope of the plot (linear regression, $F_{1,16}$ = 0.93, P > 0.1), suggesting that trail use was not influenced by topography.

We recorded 66 species in point counts over three years (Appendix 2-1). The average total species richness (S_{total}) of old road plots was 31.00 (SE 0.85), of constructed trail plots was 32.43 (0.82), and of interior plots was 29.33 (0.59). The average number of interior forest species ($S_{interior}$) detected in old road plots was 8.36 (0.38), while in constructed plots and interior plots species richness averaged 9.43 (0.24) and 9.11 (0.32), respectively. The average number of non-forest species

($S_{non\text{-}forest}$) detected in old road plots was 9.18 (0.68), while in constructed plots and interior plots non-forest species richness averaged 8.14 (0.46) and 6.78 (0.30) respectively. The average species richness of Neotropical migrant species ($S_{neotropical}$) was 15.55 (0.59) for old road plots, 18.14 (0.42) for constructed plots, and 15.56 (0.52) for interior plots (Table 2-3; Figure 2-3).

S_{total} and $S_{neotropical}$ were not associated with landscape or habitat explanatory variables (Figure 2-4). $S_{interior}$ was weakly negatively associated with Edge (BMA: EV_{edge} (SD) = -0.21 (0.36), $P_{\neq 0}$ = 0.35; Figure 2-4), while $S_{non\text{-}forest}$ was positively associated with foliage height diversity (FHD) and understory stem density (BMA: EV_{FHD} = 1.36 (0.63), $P_{\neq 0}$ = 0.94; $EV_{Undserstory}$ = 0.51 (0.61), $P_{\neq 0}$ = 0.52; Figure 2-4).

The bird community along recreational trails was best described by a 2-dimensional NMS (Stress = 0.13, Figure 2-5). Avian community structure was different among plot types (ANOSIM R = 0.36; P < 0.01, Figure 2-5). Interior plots were distinctly clustered from old road and constructed plot communities (Figure 2-5). Plot types generally clustered along axis 1, which was highly correlated with WTR (r = 0.99, P < 0.001) and GPH (r = 0.99, P < 0.001). We found that interior forest species were generally associated with narrow trail width and low trail use (Figure 2-6).

We were able to investigate the association between avian density and explanatory habitat variables for 7 interior forest species, 14 Neotropical migrants, and 7 non-forest species. Results from model averaging show that the density of interior forest and Neotropical migrant species was negatively associated with GPH and WBH (Figure 2-7, Figure 2-8). Only the density of Ovenbirds (OVEN, *Seiurus aurocapilla*) was positively associated with WBH (Figure 2-6). The density of most non-forest species was not strongly associated with trail use, except Blue Jays (BLJA, *Cyanocitta cristata*), which had a positive association with GPH (Figure 2-9). Both Brown-headed Cowbird (BHCO, *Molothrus ater*) and Blue Jay density were negatively associated with trail width (Figure 2-9). Most species' density was not strongly associated with edge forest area (Edge) or core forest area (Forest). The exceptions were Eastern Wood-Peewee (EAWP, *Contopus virens*), Ovenbird (OVEN), and Scarlet Tanager (SCTA, *Piranga olivacea*), which were all negatively associated with core forest area (Figure 2-8). The density of Wood Thrush (WOTH, *Hylocichla mustelina*), Acadian Flycatcher (ACFL, *Empidonax virescens*), Great-crested Flycatcher (GCFL, *Myiarchus crinitus*) (Figure 2-8), and Blue Jay decreased rapidly as understory stem density (Understory) increased (Figure 2-9).

2-5 Discussion

We found that overall species richness was not strongly associated with trail use, and that non-forest species richness was positively associated with forest structure, while interior forest species richness was negatively associated with edge forest area. Community composition, however, varied in association with trail use and trail width. The abundance of most species, particularly interior forest breeding species, was negatively associated with trail use and/or width.

We expected to see a decrease in interior forest species richness as trail width or use increased, due to increased disturbance from use, as suggested by Gill et al (2001). While there was no effect on interior forest species *richness* due to trails or trail use, we did find that *densities* of interior forest birds were negatively associated with trails. Our findings about the relationship of interior species richness to trail use is opposite findings in Finnish forests (Kangas et al. 2010), Colorado (Miller et al 1998), and Wyoming forests (Gutzwiller & Anderson 1999). This difference in the association with trails between abundance and richness metrics might lend support for Gill et al's (2001) second hypothesis that when habitat availability for habitat specialists (in our case, interior forest species) is limited, they may be forced to settle in less optimal habitat (e.g. close to trails). This settlement pattern suggests that habitat availability is low, and the available habitat is near trails (Bock & Jones 2004).

While interior forest species richness was not associated with trails, it was negatively associated with edge forest area, a finding in line with this guild's documented area sensitivity (Ries et al. 2004; Fletcher et al. 2007; Desrochers et al. 2010). More edge is necessarily a function of (a) complex forest shape (e.g. non-linear forest boundaries) and/or (b) increased fragmentation of forests. Our study area has experienced increased development over the last 20 years, which has increased forest fragmentation through perforation of forests by houses and associated infrastructure, such as roads and powerlines (Henschell et al, unpublished manuscript; Chapter 1). Interior forest and Neotropical species' densities were nearly all negatively associated with trail width (WBH) and trail use. Since WBH quantifies the vegetation-free area above a trail, it is likely highly related to canopy openness directly above the trail corridor. As WBH increases, canopy openness also increases, which may result in greater similarity between the trail edge and forest edge habitat, and may function in a similar way as forest fragmentation from the avian perspective. Both edge and fragmented forest support lower densities of forest songbirds (Kroodsma 1984).

Non-forest species richness, on the other hand, was associated with higher vegetation structure, in line with findings in Illinois forests (Hickman 1990). Since our study plots were all within mature forests, increased structure predominately stems from understory growth, such as shrubs and saplings, within the forest. Road edges, and wide trails on old road corridors, typically have higher vegetation volume due to increased light transmittance (Dale & Weaver 1974; Rich et al. 1994), which may provide habitat for species like Gray Catbird (*Dumetella carolinensis*) and Song Sparrow (*Melospiza melodia*).

We found that the bird community composition in interior plots was distinct from the bird communities of constructed and old road plots. Trail width and use clearly affect community structure. Interior forest species were associated with narrow (or no) tread and low to no trail use, while birds that are not interior forest species were mostly associated with wide tread width, similar to findings in Illinois and Colorado, where generalist species were more common near trails compared to areas without trails (Hickman 1990; Miller et al. 1998).

Our findings are in line with a growing body of literature suggesting that recreational trails and trail use in protected areas can have negative consequences on natural communities (e.g. plants: Dale & Weaver 1974; birds: Miller et al. 1998; protected area effectiveness: Reed & Merenlender 2008; fragmentation: Ballantyne et al. 2014). While species richness was not associated with trail types, both density of many forest-dependent species and community composition were, paralleling findings in other protected areas including a Finnish national park (Kangas et al. 2010), montane forests of Wyoming (Riffell et al. 1996; Gutzwiller & Anderson 1999), and Colorado (Miller et al. 1998).

Our results suggest that negative effects of trails on forest birds are associated with the removal of vegetation when the trail (or road) was originally constructed, as well as high levels of trail use. New forest trail construction should be avoided in interior forest habitat, and restoration of native vegetation along wide corridors through interior forest in protected areas should be prioritized. Safeguarding biodiversity is a touted benefit of establishing recreational trails (Gössling 1999; Mason et al. 2007). If the goal of safeguarding forest birds is to actually be achieved, trail construction should occur next to, but not in forest, wherever possible. When it is necessary for trails to bisect forest, their construction should be done with minimal vegetation removal, and when establishing trails along existing road corridors, consideration should be given to reducing the width of the trail through restoration of native vegetation.

2-6 Literature cited

Abràmoff MD, Magalhães PJ, Ram SJ. 2004. Image processing with ImageJ. Biophotonics international **11**:36–42.

Ballantyne M, Gudes O, Pickering CM. 2014. Recreational trails are an important cause of fragmentation in endangered urban forests: A case-study from Australia. Landscape and Urban Planning **130**:112–124.

Bock CE, Jones ZF. 2004. Avian Habitat Evaluation: Should Counting Birds Count? Frontiers in Ecology and the Environment **2**:403–410.

Burnham KP, Anderson DR. 2004. Model Selection and Multimodel Inference - A Practical Information-Theoretic Approach.

Clarke K. 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology **18**:117–143.

Curtis JT. 1959. The Vegetation of Wisconsin: An Ordination of Plant Communities. University of Wisconsin Press.

Dail D, Madsen L. 2011. Models for Estimating Abundance from Repeated Counts of an Open Metapopulation. Biometrics **67**:577–587.

Dale D, Weaver T. 1974. Trampling Effects on Vegetation of the Trail Corridors of North Rocky Mountain Forests. Journal of Applied Ecology **11**:767–772.

Desrochers A, Renaud C, Hochachka WM, Cadman M. 2010. Area-sensitivity by forest songbirds: theoretical and practical implications of scale-dependency. Ecography **33**:921–931.

ESRI. 2013. ArcGIS Desktop: Release 10.2. Environmental Systems Research Institute, Redlands, CA.

Fiske I, Chandler R. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software **43**:1–23.

Fletcher J Robert J, Ries L, Battin J, Chalfoun AD. 2007. Canadian Journal of Zoology **85**:1017–1030.

Gill JA, Norris K, Sutherland WJ. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation **97**:265–268.

Gössling S. 1999. Ecotourism: a means to safeguard biodiversity and ecosystem functions? Ecological Economics **29**:303–320.

Gutzwiller KJ, Anderson SH. 1999. Spatial Extent of Human-Intrusion Effects on Subalpine Bird Distributions. The Condor **101**:378–389.

Hickman S. 1990. Evidence of edge species attraction to nature trails within deciduous forest. Natural Areas Journal **10**:3–5.

Hoeting JA, Madigan D, Raftery AE, Volinsky CT. 2000. Bayesian model averaging: A tutorial (vol 14, pg 382, 1999). Statistical Science **15**:193–195.

Homer C, Dewitz, Jon, Yang J, Jin S, Danielson P, Xian G, Coulston JW, Wickham JD, Megown K. 2011. Completion of the 2011 National Land Cover Database for the conterminous United States-Representing a decade of land cover change information. Photogrammetric engineering and remote sensing **81**:345–354.

Kangas K, Luoto M, Ihantola A, Tomppo E, Siikamäki P. 2010. Recreation-induced changes in boreal bird communities in protected areas. Ecological Applications **20**:1775–1786.

Karp DS, Guevara R. 2011. Conversational Noise Reduction as a Win–Win for Ecotourists and Rain Forest Birds in Peru. Biotropica **43**:122–130.

Kroodsma RL. 1984. Effect of Edge on Breeding Forest Bird Species. The Wilson Bulletin **96**:426–436.

Mason J, Moorman C, Hess G, Sinclair K. 2007. Designing suburban greenways to provide habitat for forest-breeding birds. Landscape and Urban Planning **80**:153–164.

McCune B, Grace JB, Urban DL. 2002. Analysis of ecological communities. MjM software design Gleneden Beach, Oregon.

Miller SG, Knight RL, Miller CK. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications **8**:162–169.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2013. vegan: Community Ecology Package. Available from http://CRAN.R-project.org/package=vegan.

Peel MC, Finlayson BL, Mcmahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences Discussions **4**:439–473.

Peterjohn BG, Sauer JR. 1993. North American Breeding Bird Survey annual summary 1990-1991. Bird Populations **1**:52–67.

Pidgeon AM, Radeloff VC, Flather CH, Lepczyk CA, Clayton MK, Hawbaker TJ, Hammer RB. 2007. Associations of forest bird species richness with housing and landscape patterns across the USA. Ecological Applications **17**:1989–2010.

R Core Development Team. 2013. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Raftery AE. 1995. Bayesian model selection in social research. Sociological methodology **25**:111–164.

Ralph CJ, Sauer JR, Droege S. 1995. Managing and monitoring birds using point counts: standards and applications. Pages 161–168in C. J. Ralph, S. Droege, and J. R.

Sauer, editors. Monitoring bird populations by point counts. U.S. Forest Service General Technical Report PSW-GTR-149. U.S. Forest Service, Albany, CA.

Reed SE, Merenlender AM. 2008. Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. Conservation Letters **1**:146–154.

Rich AC, Dobkin DS, Niles LJ. 1994. Defining Forest Fragmentation by Corridor Width: The Influence of Narrow Forest-Dividing Corridors on Forest-Nesting Birds in Southern New Jersey. Conservation Biology **8**:1109–1121.

Ries L, Fletcher RJ, Battin J, Sisk TD. 2004. Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. Annual Review of Ecology, Evolution, and Systematics **35**:491–522.

Riffell SK, Gutzwiller KJ, Anderson SH. 1996. Does Repeated Human Intrusion Cause Cumulative Declines in Avian Richness and Abundance? Ecological Applications **6**:492–505.

Tabachnick BG, Fidell LS. 2012. Using Multivariate Statistics6 edition. Pearson, Boston.

Tennessee Department of Environment and Conservation. 2007. Pathways to Trail Building. Page 40. Tennessee Department of Environment and Conservation, Nashville, TN.

US Geological Survey Gap Analysis Program (GAP). 2012, November 30. Protected Areas Database of the United States (PADUS) version 1.3. USGS Gap Analysis Program (GAP). Available from http://gapanalysis.usgs.gov/PADUS (accessed December 15, 2013).

Vogt P, Riitters KH, Estreguil C, Kozak J, Wade TG. 2007. Mapping spatial patterns with morphological image processing. Landscape Ecology **22**:171–177.

Zar JH. 2010. Biostatistical Analysis. Prentice Hall, Upper Saddle River, New Jersey USA.

2-7 Tables

Table 2-1 Correlation between selected explanatory variables. The Upper triangle shows Pearson's correlation coefficient (*r*). The lower triangle shows *p* value of the t-test for significance of the correlation. Significant values are in bold (α = 0.05).

	WTR	**WBH**	**GPH**	**FHD**	**OPEN**	**Edge**	**Forest**	**Understory**
WTR		0.85	0.83	0.27	0.11	0.36	-0.07	-0.15
WBH	**0.00**		0.53	0.27	0.26	0.45	0.04	-0.32
GPH	**0.00**	**0.03**		0.34	0.14	0.23	-0.08	0.19
FHD	0.21	0.24	0.14		-0.03	0.27	-0.14	-0.05
OPEN	0.86	0.90	0.89	0.55		-0.15	0.08	0.12
Edge	0.14	0.14	0.23	0.17	0.28		-0.45	0.10
Forest	0.53	0.76	0.36	0.35	0.71	**0.02**		-0.35
Understory	0.27	0.08	0.86	0.65	0.96	0.93	0.12	

Table 2-2 Summary statistics for explanatory variables. Mean measurement for each plot type, followed by the standard error in parentheses. *F* is the *F*-statistic from analysis of variance on 2 and 24 degrees of freedom.

Variable	Constructed	Interior	Old road	$F_{2,24}$
WTR	0.66 (0.04)	0 (0)	1.94 (0.11)	71.9*
WBH	2.48 (0.09)	0 (0)	4.51 (0.19)	108.3*
GPH	0.75 (0.11)	0 (0)	1.87 (0.26)	10.7*
FHD	3.11 (0.06)	2.97 (0.04)	3.17 (0.03)	2.1
OPEN	0.2 (0.01)	0.17 (0.01)	0.19 (0.01)	1.4
Edge	0.11 (0.01)	0.07 (0.02)	0.15 (0.01)	3.6*
Forest	0.37 (0.02)	0.39 (0.02)	0.38 (0.01)	0.2
Understory	70919.44 (5554.3)	74979.66 (2667.52)	63175.83 (5501.51)	0.6

* Significant difference among groups ($\alpha = 0.05$)

Table 2-3 Summary statistics for bird guild richness. Mean measurement for each plot type, followed by the standard error in parentheses. *F* is the *F*-statistic from analysis of variance on 2 and 24 degrees of freedom.

Guild	Constructed	Interior	Old road	$F_{2,24}$
Total	32.43 (0.82)	29.33 (0.59)	31 (0.85)	1.2
Interior	9.43 (0.24)	9.11 (0.33)	8.36 (0.38)	0.9
Non-forest	8.14 (0.46)	6.78 (0.3)	9.18 (0.68)	1.9
Neotropical	18.14 (0.42)	15.56 (0.52)	15.55 (0.59)	2.3

2-8 List of figures

univariate relationship between density and the indicated explanatory variable, holding all other variables at their mean.

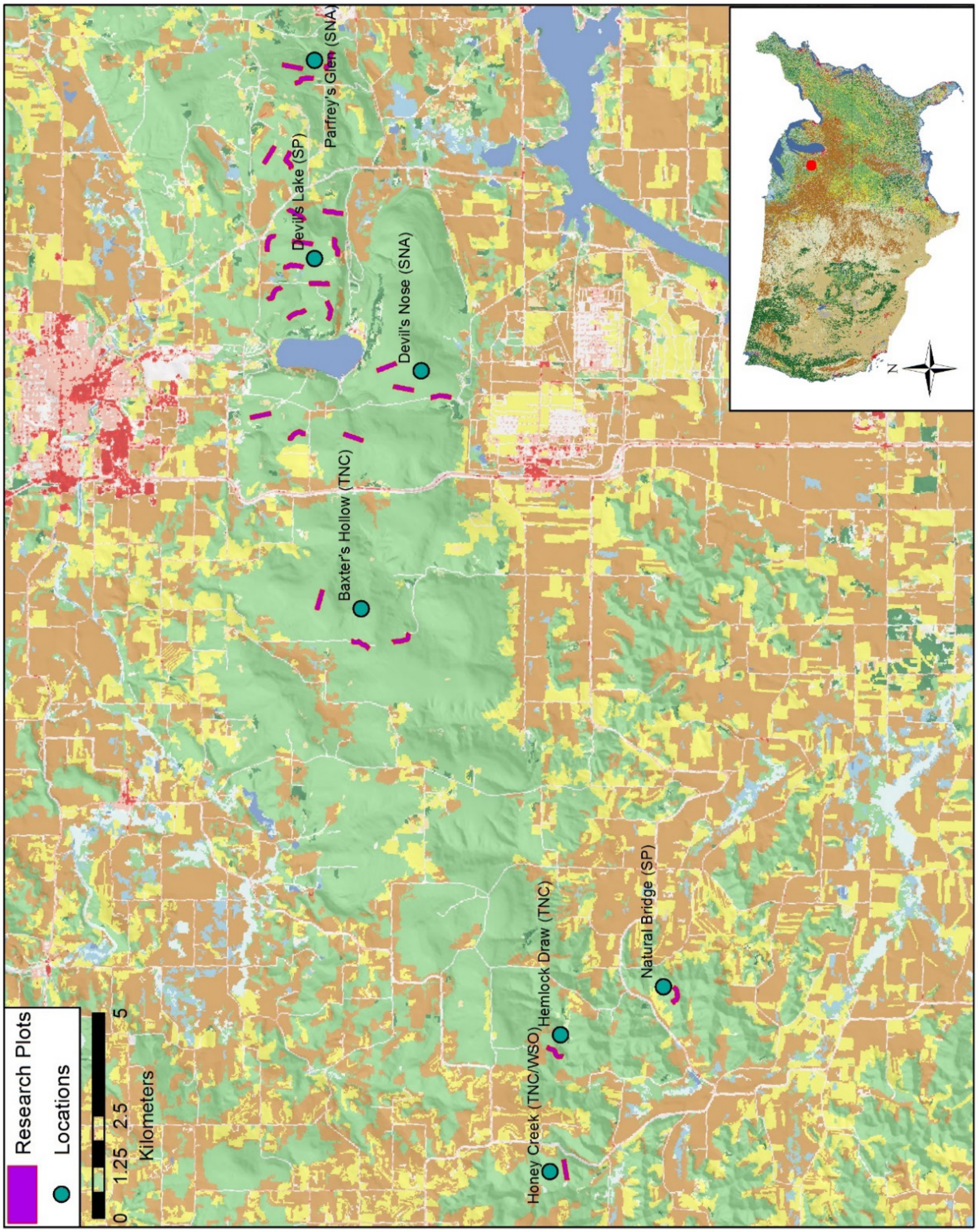

Research Plots
Locations
0 1.25 2.5 5
Kilometers
Parfrey's Glen (SNA)
Devil's Lake (SP)
Devil's Nose (SNA)
Baxter's Hollow (TNC)
Hemlock Draw (TNC)
Honey Creek (TNC/WSO)
Natural Bridge (SP)
N

Figure 2-1

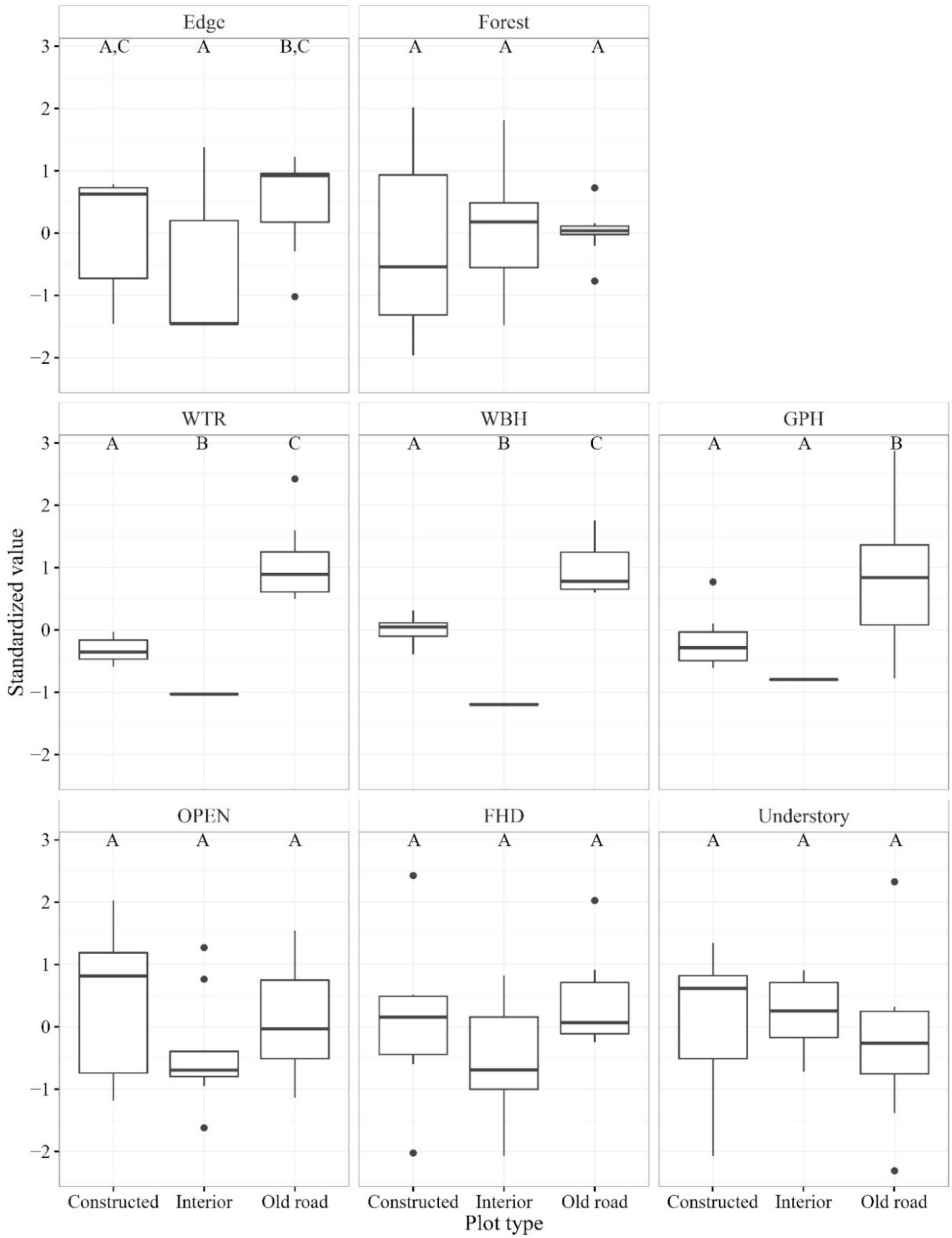

Edge
A,C
A
B,C
Forest
A
A
A
WTR
A
B
C
WBH
A
B
C
GPH
A
A
B
OPEN
A
A
A
FHD
A
A
A
Understory
A
A
A
Standardized value
3
2
1
0
−1
−2
Constructed
Interior
Old road
Plot type

Figure 2-2

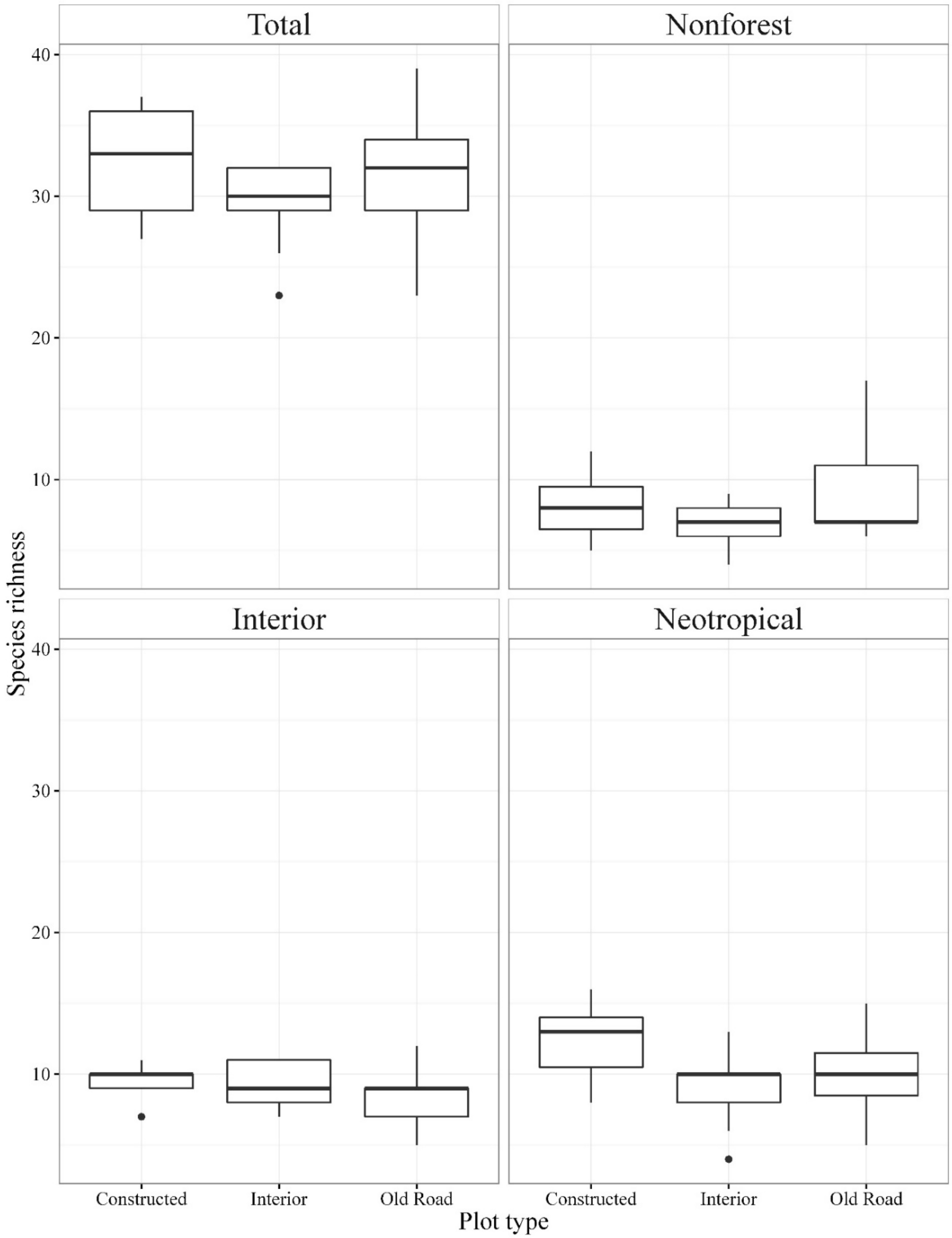

Total
Nonforest
Interior
Neotropical
Species richness
40
30
20
10
Constructed
Interior
Old Road
Plot type

Figure 2-3

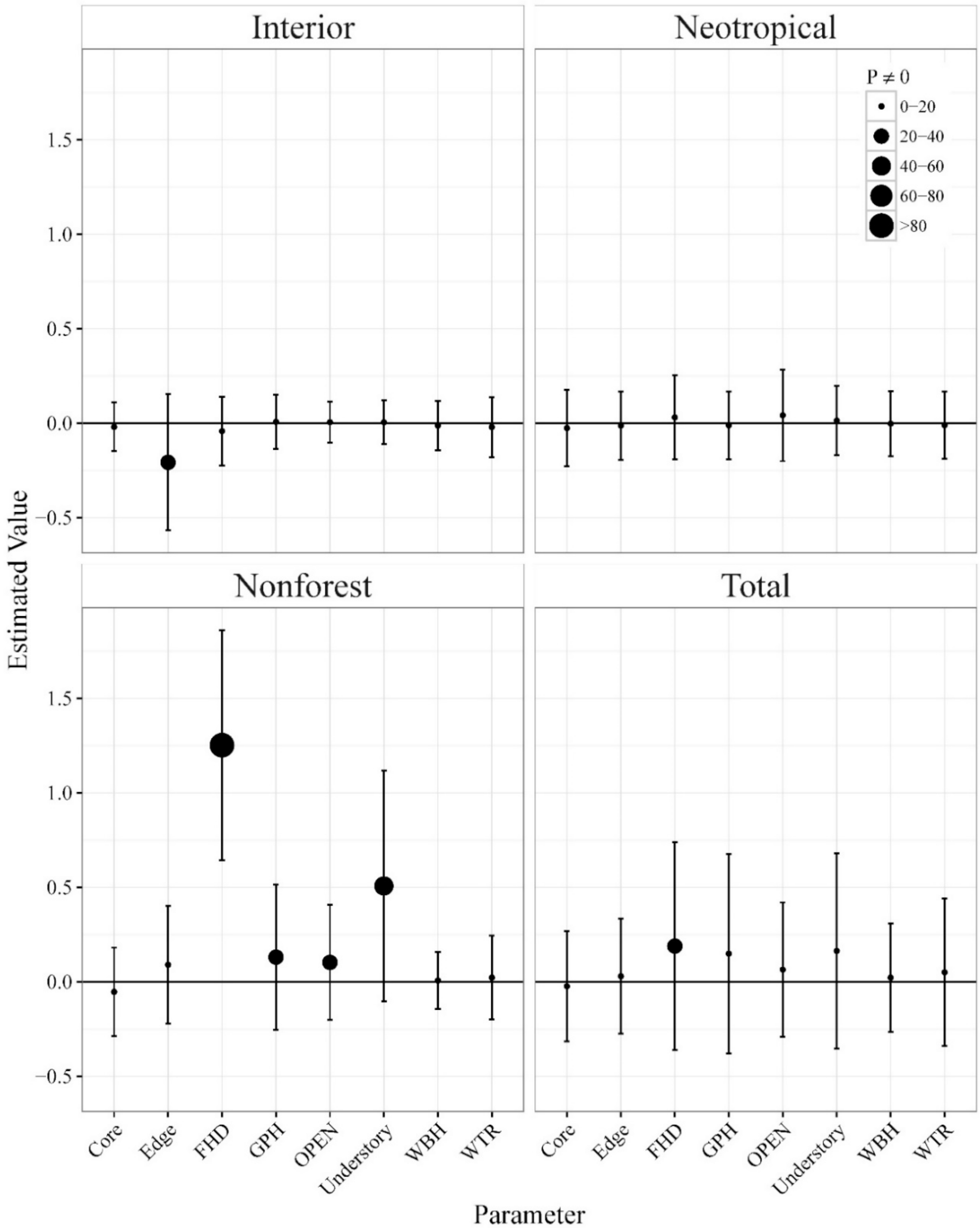
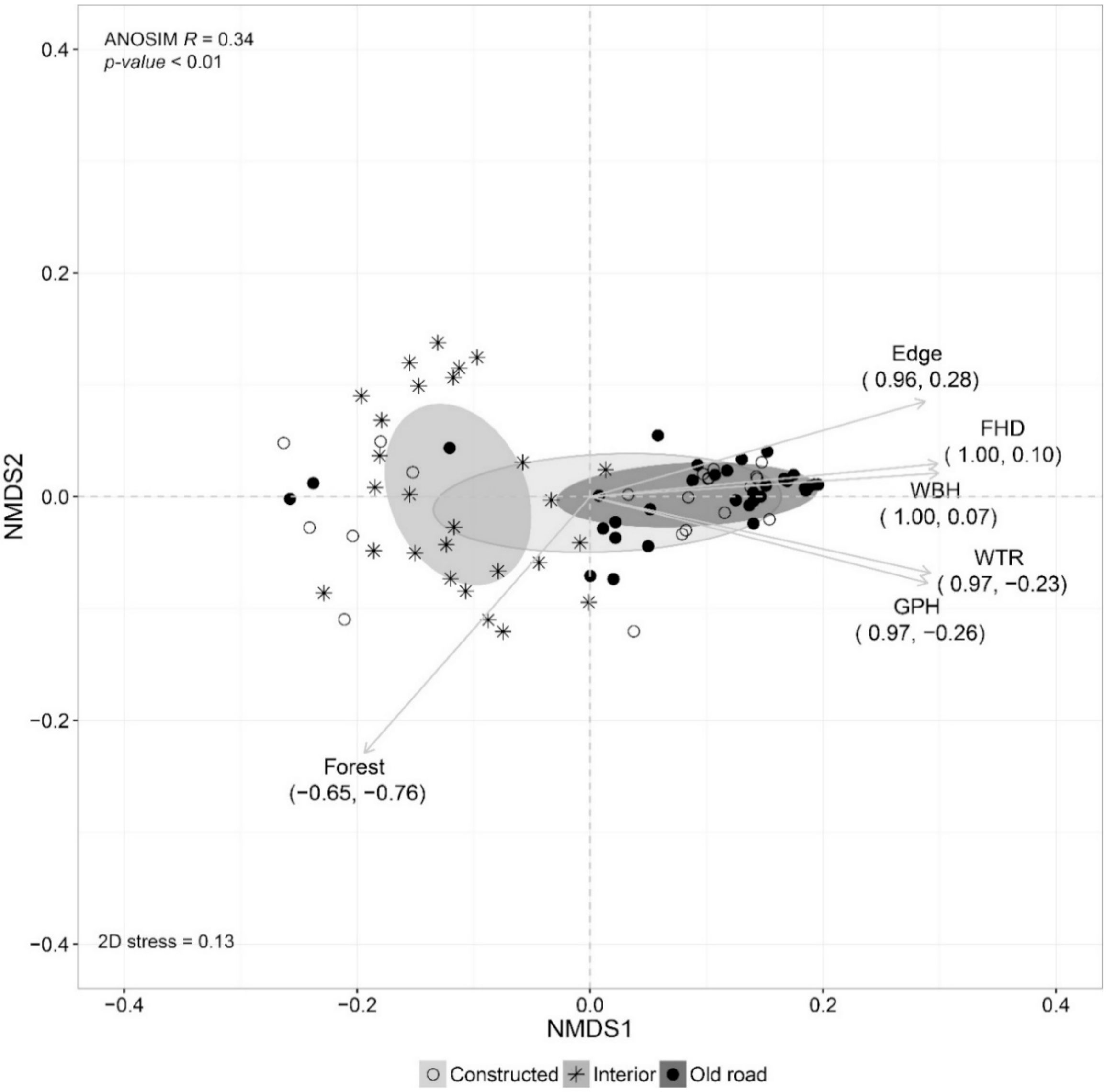

Interior
Neotropical
Nonforest
Total
P ≠ 0
0−20
20−40
40−60
60−80
>80
Estimated Value
1.5
1.0
0.5
0.0
−0.5
Core
Edge
FHD
GPH
OPEN
Understory
WBH
WTR
Parameter

Figure 2-4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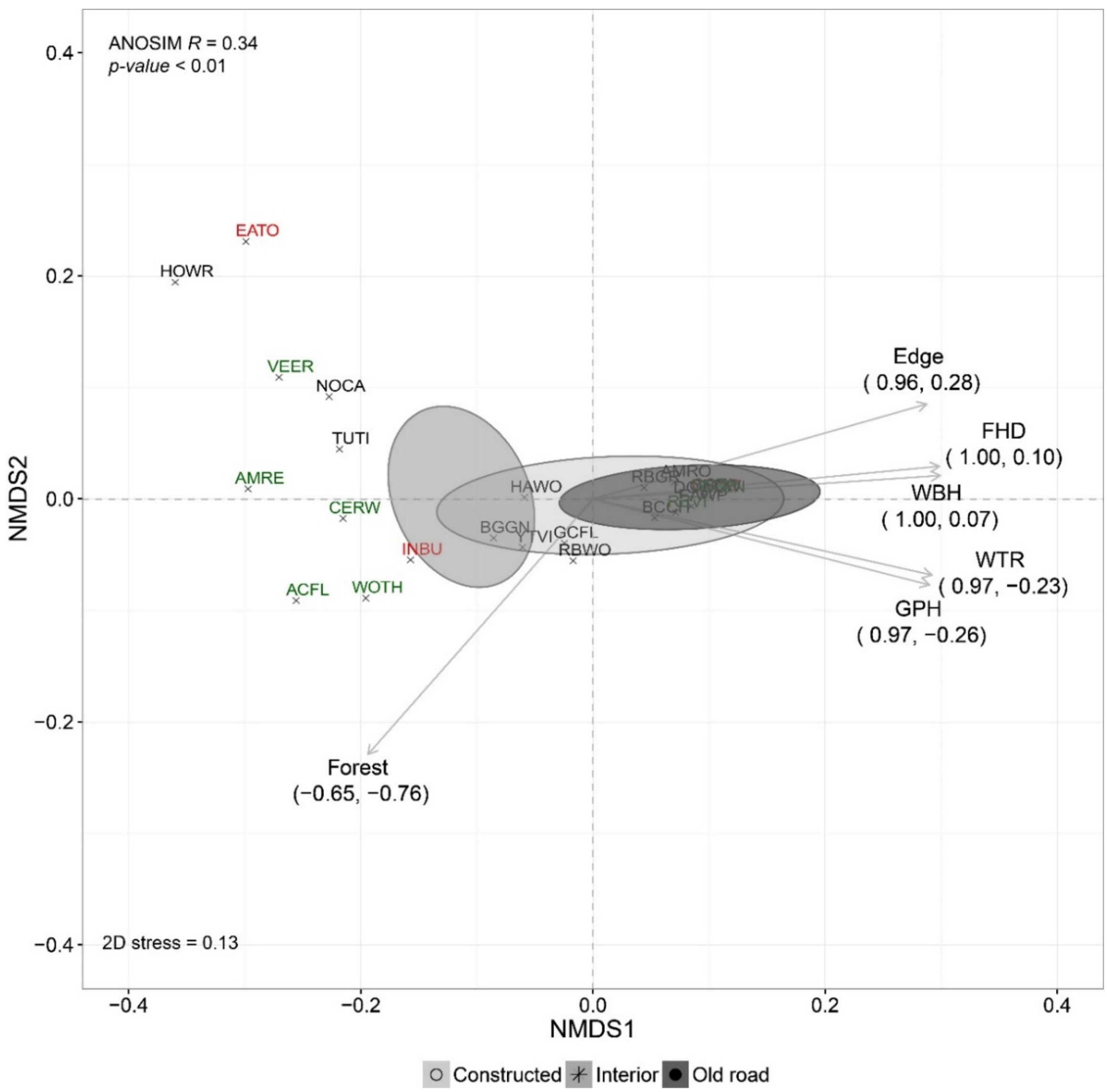
p-value < 0.01
Edge
(0.96, 0.28)
FHD
(1.00, 0.10)
WBH
(1.00, 0.07)
WTR
(0.97, −0.23)
GPH
(0.97, −0.26)
Forest
(−0.65, −0.76)
2D stress = 0.13
NMDS1
NMDS2
0.4
0.2
0.0
−0.2
−0.4
Constructed
Interior
Old road

Figure 2-5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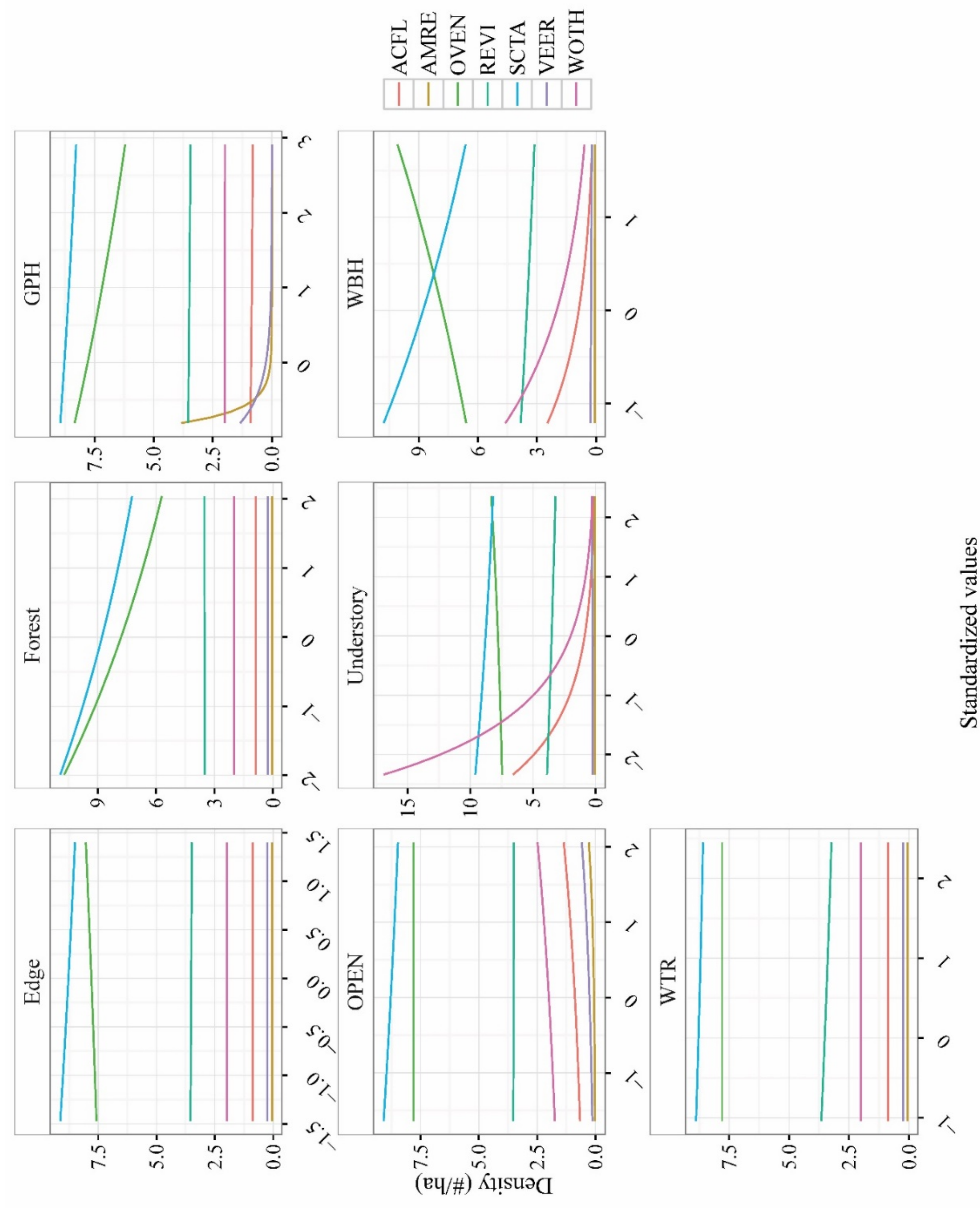
p-value < 0.01
EATO
HOWR
VEER
NOCA
TUTI
AMRE
CERW
INBU
ACFL
WOTH
HAWO
BGGN
YTVI
GCFL
RBWO
AMRO
BCCH
Edge
(0.96, 0.28)
FHD
(1.00, 0.10)
WBH
(1.00, 0.07)
WTR
(0.97, −0.23)
GPH
(0.97, −0.26)
Forest
(−0.65, −0.76)
2D stress = 0.13
NMDS1
NMDS2
Constructed
Interior
Old road

Figure 2-6



Edge
Forest
GPH
OPEN
Understory
WBH
WTR
ACFL
AMRE
OVEN
REVI
SCTA
VEER
WOTH
Density (#/ha)
Standardized values

Figure 2-7

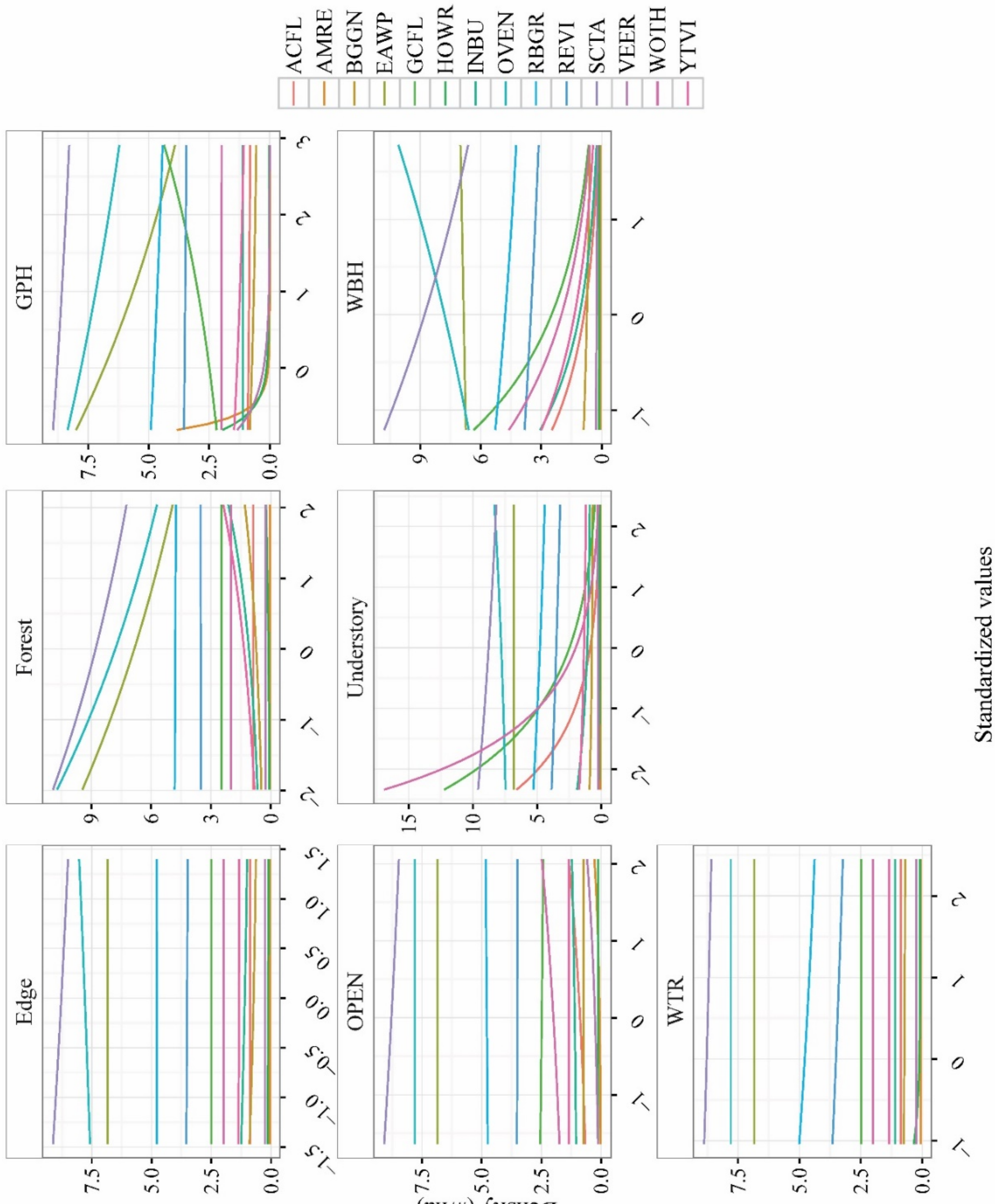

Edge
Forest
GPH
OPEN
Understory
WBH
WTR
Density (#/ha)
Standardized values
ACFL
AMRE
BGGN
EAWP
GCFL
HOWR
INBU
OVEN
RBGR
REVI
SCTA
VEER
WOTH
YTVI

Figure 2-8

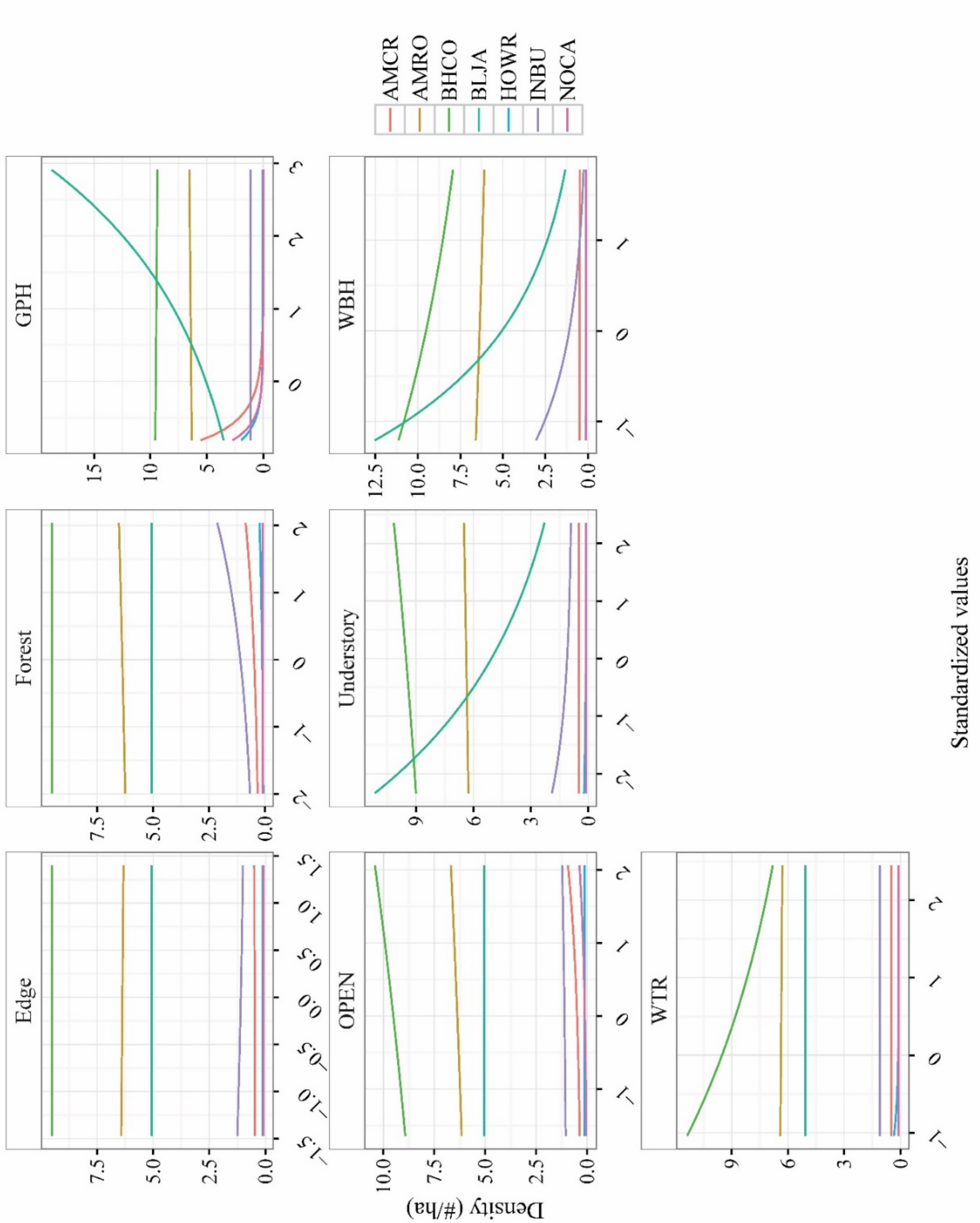

Edge
Forest
GPH
OPEN
Understory
WBH
WTR
AMCR
AMRO
BHCO
BLJA
HOWR
INBU
NOCA
Density (#/ha)
Standardized values

Figure 2-9

2-9 List of Appendices

Appendix 2-1 Species recorded over three years of point counts along trail plots in the Baraboo Hills of Wisconsin. AOU code is the unique 4-letter abbreviation for each bird species. Common name is the unique American Ornithologists' Union (AOU) common name for each bird species. Guild associations follow the common name (Peterjohn and Sauer 1993, Pidgeon et al 2007).

Appendix 2-2 Candidate models for estimating species detectability and density.

Appendix 2-1

AOU code	Common name	Scientific name	Interior	Nonforest	Neotropical Migrant
ACFL	Acadian Flycatcher	*Empidonax virescens*	X	--	X
AMCR	American Crow	*Corvus brachyrhynchos*	--	X	--
AMGO	American Goldfinch	*Spinus tristis*	--	X	--
AMRE	American Redstart	*Setophaga ruticilla*	X	--	X
AMRO	American Robin	*Turdus migratorius*	--	X	--
BBCU	Black-billed Cuckoo	*Coccyzus erythropthalmus*	--	--	X
BCCH	Black-capped Chickadee	*Poecile atricapillus*	--	--	--
BGGN	Blue-gray Gnatcatcher	*Polioptila caerulea*	--	--	X
BHCO	Brown-headed Cowbird	*Molothrus ater*	--	X	--
BLJA	Blue Jay	*Cyanocitta cristata*	--	X	--
BRCR	Brown Creeper	*Certhia americana*	X	--	--
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	--	--	--
CERW	Cerulean Warbler	*Setophaga cerulea*	X	--	X
DOWO	Downy Woodpecker	*Picoides pubescens*	--	--	--
EATO	Eastern Towhee	*Pipilo erythrophthalmus*	--	X	--
EAWP	Eastern Wood-Pewee	*Contopus virens*	--	--	X
GCFL	Great Crested Flycatcher	*Myiarchus crinitus*	--	--	X
HAWO	Hairy Woodpecker	*Picoides villosus*	--	--	--
HOWA	Hooded Warbler	*Setophaga citrina*	X	--	X
HOWR	House Wren	*Troglodytes aedon*	--	X	X
INBU	Indigo Bunting	*Passerina cyanea*	--	X	X
LEFL	Least Flycatcher	*Empidonax minimus*	X	--	X
MODO	Mourning Dove	*Zenaida macroura*	--	X	--
NOCA	Northern Cardinal	*Cardinalis cardinalis*	--	X	--

AOU code	Common name	Scientific name	Interior	Nonforest	Neotropical Migrant
NOFL	Northern Flicker	*Colaptes auratus*	--	--	--
OVEN	Ovenbird	*Seiurus aurocapilla*	X	--	X
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	X	--	--
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	--	--	X
RBWO	Red-bellied Woodpecker	*Melanerpes carolinus*	--	--	--
REVI	Red-eyed Vireo	*Vireo olivaceus*	X	--	X
RTHU	Ruby-throated Hummingbird	*Archilochus colubris*	--	--	X
SCTA	Scarlet Tanager	*Piranga olivacea*	X	--	X
TUTI	Tufted Titmouse	*Baeolophus bicolor*	--	--	--
VEER	Veery	*Catharus fuscescens*	X	--	X
WBNU	White-breasted Nuthatch	*Sitta carolinensis*	--	--	--
WITU	Wild Turkey	*Meleagris gallopavo*	--	--	--
WIWR	Winter Wren	*Troglodytes hiemalis*	X	--	--
WOTH	Wood Thrush	*Hylocichla mustelina*	X	--	X
YBCU	Yellow-billed Cuckoo	*Coccyzus americanus*	--	--	X
YTVI	Yellow-throated Vireo	*Vireo flavifrons*	--	--	X

Appendix 2-2

Detectability models	Density models
p(OrdDate+Start+Wind+Obs)	λ(OPEN)
p(OrdDate+Start+Obs)	λ(Shrub)
p(Start+Wind+Obs)	λ(Edge500m)
p(OrdDate+Wind+Obs)	λ(Core5km)
p(OrdDate+Obs)	λ(WBH)
p(Start+Obs)	λ(WTR)
p(Wind+Obs)	λ(GPH)
p(OrdDate)	λ(Shrub+OPEN)
p(Start)	λ(Shrub+OPEN+WTR)
p(Wind)	λ(Shrub+OPEN+WBH)
p(Obs)	λ(Shrub+OPEN+GPH)
	λ(Shrub+WTR)
	λ(Shrub+WBH)
	λ(Shrub+GPH)
	λ(OPEN+WTR)
	λ(OPEN+WBH)
	λ(OPEN+GPH)
	λ(Edge500m+Core5km+WTR)
	λ(Edge500m+Core5km+WBH)
	λ(Edge500m+Core5km+GPH)
	λ(Edge500m+GPH)
	λ(Edge500m+WTR)
	λ(Edge500m+WBH)
	λ(Core5km+WTR)
	λ(Core5km+WBH)
	λ(Core5km+GPH)
	λ(WBH+GPH)
	λ(WBH+GPH+Shrub)
	λ(WBH+GPH+OPEN)
	λ(WBH+GPH+Edge500m)
	λ(WBH+GPH+Core5km)

Chapter 3: Recreational trails and trail use reduce forest passerine nest success in protected areas

3-1 Abstract

Protected areas are typically created to meet a number of goals including providing recreation opportunities and habitat for wild species. Outdoor recreation in protected areas is considered an ecosystem service, but may undermine habitat conservation. Here, we consider the effects of hiking trails and the amount of trail use, as well local landscape patterns, on the nest daily survival rate (DSR), a measure of nest success, of three forest passerines. We found that Acadian flycatcher (*Empidonax virescens*) DSR was negatively associated with date, trail use, trail width, and brood parasitism. Wood thrush (*Hylocichla mustelina*) DSR was positively associated with the amount of core forest in the local landscape, but was higher along roads converted to trails compared to constructed trails, which were much narrower than old road trails. American robin (*Turdus migratorius*) DSR was positively associated with the area of forest edge and negatively associated with trail use. We also found that Acadian flycatcher DSR decreased with date near trails, but did not decrease in areas without trails. All three species typically begin nesting before the peak of recreational trail use throughout their breeding range, so the establishment of

territories followed by increased trail use may result in an ecological trap in areas with heavy recreational use. Trail use in protected areas with dense trail networks might have population–level consequences in landscapes that do not have source populations outside heavily used areas. Land managers can use this information to better address both access and species conservation in protected areas.

Keywords: Daily survival rate, trails, Acadian flycatcher (*Empidonax virescens*), American robin *(Turdus migratorius*), wood thrush (*Hylocichla mustelina*), Bayesian model averaging, disturbance

3-2 Introduction

Outdoor recreation is an ecosystem service provided frequently in natural or semi–natural areas (Chan, Shaw, Cameron, Underwood, & Daily, 2006) and is an important benefit to local economies. Nearly $700 billion dollars are spent on recreation annually in the United States, about 30% of which is spent by recreational trail users (Outdoor Industry Association, 2012). Participation in hiking increased 8–fold between 1970 and 2000 in the United States (Reed & Merenlender, 2008). Many areas where recreation is permitted or encouraged are protected areas, such as national, state or local parks, forests or wildlife refuges.

Hiking trails provide the primary access into protected area interiors. These trails are typically established by one of two means. Constructed trails have a tread, or area devoid of vegetation, of approximately 0.6 m. The narrow tread width limits the removal of vegetation during construction, which tends to minimize changes in habitat structure along trail corridors (Hesselbarth, Vachowski, & Davies, 2007). Therefore, constructed trails in forested areas usually retain a closed canopy. The second method of trail development is to convert roads to trails. Old road trails tend to have a much wider tread than constructed trails, and in forested areas old road trails often have an open or broken canopy overhead due to vegetation removal during the initial construction of the road.

Nest success is a critical demographic process for the persistence of bird populations. Nest success, and ultimately species' persistence, is affected by a number of different factors including weather, nest predation, and brood parasitism; the latter two may be strongly affected by landscape configuration (Martin, 1995; Ricklefs, 1969; Zuckerberg & Porter, 2010). Human disturbance can compound the negative effects of these natural factors by altering birds' behavior (Campbell, 2011; Miller, Knight, & Miller, 2001; Smith-Castro & Rodewald, 2010). Nesting birds react to disturbance near their nest in a variety of ways, often depending on the stage of the nesting cycle. Disturbance early in the nesting cycle, such as during the building or laying stage, may result in abandonment, but as investment in a nest increases nesting birds are more likely to tend the nest and young despite disturbance (Garrettson, Richkus, Rohwer, & Johnson, 2010). The physical presence of any recreationist, which may be perceived as a potential predator (Frid & Dill, 2002), can cause nesting birds to fly away, particularly if the human is very close to a nest (Smith-Castro & Rodewald, 2010). For a bird, being flushed from the nest results in altered time budgets, potentially including decreased feeding rates, nest attendance (Verhulst, Oosterbeek, & Ens, 2001) as well as elevated levels of corticosterone (Ouyang, Quetting, & Hau, 2012). These behavioral and hormonal changes can result in decreased reproductive rates (Ouyang et al., 2012; Strasser & Heath, 2013;

Verhulst et al., 2001), and can have adverse population–level consequences (Kerbiriou et al., 2009).

Habitat loss and fragmentation of forests create ecotones, or habitat discontinuities. As a landscape feature, ecotones have become increasingly common since European settlement due to forest clearing and increased agriculture (Curtis, 1959). Ecotones between forest and other habitat types are attractive to predators of birds and bird nests, as well as brood parasites (Gates & Gysel, 1978; Neher, Asmussen, & Lovell, 2013; Rich, Dobkin, & Niles, 1994). Forest passerines in the eastern United State evolved within the context of unfragmented forests, but in the relatively recently created landscape of forest fragments and ecotones, predation by avian predators, such as blue jays (*Cyanocitta cristata*) and American crows (*Corvus brachyrhynchos*), and brood parasitism by brown-headed cowbirds (*Molothrus ater*) may increase (Chapa-Vargas & Robinson, 2013; Etterson, Greenberg, & Hollenhorst, 2014; Gates & Gysel, 1978). Wide corridors through forests, such as those associated with roads and powerlines, exhibit some features of ecotones, including increased vegetation volume along road edges and increased canopy openness (Rich et al., 1994). Recreational trails have been identified as a source of habitat fragmentation (Ballantyne, Gudes, & Pickering, 2014), and, given the structural similarities between some trail corridors and other linear forest corridors, might similarly degrade the quality of forest habitat for breeding passerines.

We investigated how trails, trail use, and landscape context affected nest daily survival rate (DSR), a measure of nest success of forest passerines. Our overarching objective was to determine the relative importance of the physical presence of recreational trails and the amount of recreational use of trails in nest success of passerines. Our specific objectives were to (1) quantify the range of landscape and trail characteristics and recreational trail use and (2) determine whether nest daily survival rates for three forest passerines nests is affected by trail characteristics, recreational use, or the characteristics of the surrounding landscape. We hypothesized that DSR would decrease with increasing trail width and amount of use and would increase with the distance of nests from trails.

3-3 Methods

3-3.1 Study area

The Baraboo Hills, located in southern Wisconsin (Figure 3-1), encompass approximately 58,000 ha and contain nearly 22,000 ha of primarily deciduous forest (Baraboo Range Preservation Association, 2014). Approximately 50% of the forested area of the Baraboo Hills is protected by state and nongovernmental organizations, and include recreational trails for hiking. Devil's Lake State Park, the most visited state park in Wisconsin, is located in the Baraboo Hills, with 1.5 million visitors every year and nearly 50 km of recreational trails (Wisconsin Department of Natural Resources, 2015).

We established 43 study plots in forested habitat distributed across the Baraboo Hills. In 2009, eight plots were randomly located along unmarked trails with evidence of human use, which were very similar in all respects to constructed trails, while the other eight were randomly located along old road trails. These 16 study plots were 200 meters long, 400 meters wide, and bisected by a trail (Appendix 3-1).Twenty-seven different plots were monitored in 2012–2013. Eighteen were randomly located along marked trails, 9 of which were along old road trails, the other 9 were along constructed trails. Nine were randomly located in the forest interior, and functioned as controls. All 27 plots in 2012–2013 were 500 m long, 100 meters wide. The 18 plots located on trails were bisected along their length by a trail (Appendix 3-1). All plots were at least 100 m from any nonforested habitat and at least 250 m from another plot.

3-3.2 FOCAL SPECIES AND NEST MONITORING

We searched for and monitored nests of three forest-breeding passerines, Acadian flycatcher (*Empidonax virescens*), American robin (*Turdus migratorius*), and wood thrush (*Hylocichla mustelina*), within our study plots. We chose these species based on their range and life history characteristics. Specifically, all three species are found in forested habitats in the eastern United States. Acadian flycatcher and wood thrush are acceptors of brood parasite eggs, are forest interior species, and vulnerable to the effects of habitat fragmentation, all of which we speculate could be affected by trails (Evans, Gow, Roth, Johnson, & Underwood, 2011; Whitehead & Taylor, 2002). American robins are habitat generalists, and found throughout the fragmentation gradient from interior forests to urban areas, and so may be better able to cope with trails and trail use (Vanderhoff, Sallabanks, Rex, & James, Frances C., 2014). All three might benefit from small forest openings, such as trails, for foraging, since Acadian flycatchers needs unobstructed air space in which to successfully capture aerial insects, while American robins and wood thrushes forage for invertebrates in the litter layer of open forest understories (Evans et al., 2011; Vanderhoff et al., 2014; Whitehead & Taylor, 2002).

We used both visual cues and systematic searching to locate nests (Martin & Geupel, 1993). We recorded a GPS coordinate near each nest and visually inspected nests with a mirror attached to a 3 m telescoping pole to determine the stage (building, laying, incubating, or nestlings present). If the nest was beyond the reach of the pole, we used behavioral cues to determine the nest stage. We visited nests approximately every 4 days and recorded the number of eggs, number of juveniles, and number of brown-headed cowbird eggs or juveniles at each visit. We recorded the fate of the nest once it was inactive. Nests were considered inactive when juveniles had fledged, or the nest was abandoned, depredated, or otherwise destroyed. We calculated nest density (nests/ha) for each species using nests which were located within the plot boundaries.

3-3.3 Trail and Landscape characteristics

We recorded two measures of trail width at three points along the trail in each plot: the tread width (WTR) and the width of the open space (i.e. without vegetation) at 1.4 m from the ground (WBH). We averaged each set of measurements, resulting in a mean WTR and WBH for each plot. We also walked all of the trails with a GPS to record their length and subsequently determine trail density (km/km^2) within the forest patches containing our study plots.

We used the nest location GPS point to calculate the distance from each nest to the nearest trail (TrailDist) in a GIS. We also calculated the area of edge forest (Edge Area), defined as the 60 m of forest nearest any nonforest land cover class, within 500 m of each nest as a local-scale measure of forest fragmentation (Chapa-Vargas, Robinson, & Johnson, 2007). Finally, we calculated area of core forest (Core Area) defined as the forested land cover excluding edge forest, within 10 km of each nest, because the effects of nest predation and brood parasitism on forest songbird nest success has been well explained at the scale extent of 10 km (Lloyd, Martin, Redmond, Langner, & Hart, 2005). We calculated these metrics using morphological spatial pattern analysis (Soille & Vogt, 2009) on the National Land Cover Database for the year 2011 (Jin et al., 2013). We used the Guidos Toolbox for MSPA using the following settings: 4-cell neighborhood, edge width of 2 pixels (60 m), no transition, and no intext cell calculations to calculate the area of edge and the area of core forest (Vogt, 2014).

3-3.4 TRAIL USE MONITORING

In 2009, we counted all groups of recreationists that we detected using trails while conducting field work (approximately 75 hours of monitoring per week, distributed among daylight hours). In 2012 and 2013, we used microprocessor-based passive infrared trail monitors to record trail use, which we built from readily available open source hardware components. The monitors were positioned with the passive infrared sensor perpendicular to the trail. Each time an individual or group of trail users passed the sensor, the device recorded the time at which the activity occurred. We included only trail use events recorded between 0600 and 2100, capturing the majority of recreational use while reducing the chance of misclassifying wildlife on the trails as human users. We sampled trail use three times during the breeding season (15 May to 10 July) at each trail plot, with order of sampling randomly determined during each of the three sampling bouts. For each trail we determined a level of recreational use, reported as the average number of trail user groups per hour (GPH) throughout the breeding season. Our monitors recorded zero use of some trails, yet we did see evidence of use on these trails, such as footprints and litter. Failure to record these trail users occurred because the trails were not continuously monitored. It was important to include a value for human traffic where evidence indicated use, so we adopted the conservative rule of assigning to these trails a GPH value of one-half the lowest trail GPH recorded on all other trails.

3-3.5 Statistical analysis

We tested for differences between old road trails and constructed trails in GPH, WTR, and WBH using Bayesian estimation with a burn-in of 1000 MCMC chains, and 10,000 chains (Kruschke, 2013). We considered the means to be statistically different between trail types if the 95% highest density interval (HDI) did not overlap zero (Kruschke, 2013). The 95% HDI contains 95% of the distribution of sample differences from the MCMC. We also used Bayesian estimation to test whether there were differences in distance to constructed or old road trails, and differences in core forest area and edge forest area in the landscapes surrounding the nests of each species (Kruschke, 2013). To better understand patterns in trail use, we used linear regression to investigate the relationship between WTR and GPH as well as the relationship between WBH and GPH (Zar, 2010). We used analysis of variance to investigate whether there were differences in nest density (# nests/ha) for each species among interior, constructed and old road plots.

Nest daily survival rate (DSR) is an estimate of the probability that a nest survives a single day, given the number of days between each monitoring visit (the exposure period) and additional predictive factors (Mayfield, 1961; Shaffer, 2004). We used logistic exposure, which is a logit transform of exposure period nest fate (0 = failure, 1 = success) as a function of model covariates (Shaffer, 2004). Nest success (the proportion of nests that fledge at least one juvenile) can be calculated as follows:

$$Nest\ success\ = \frac{length\ of\ the\ nesting\ period^{DSR}}{100}$$

where the length of the nesting period for Acadian flycatcher, wood thrush, and American robin averages 29, 26, and 26 days, respectively (Evans et al., 2011; Vanderhoff et al., 2014; Whitehead & Taylor, 2002).

We used a Bayesian model averaging framework to investigate the effects of trails, trail use, and landscape characteristics on the DSR for each of our three species. Bayesian model averaging accounts for uncertainty in model selection processes when calculating estimates for parameters, particularly when there are a large number of potential model covariates (Raftery, 1995). This method provides improved predictive power over frequentist model averaging (Hoeting, Madigan, Raftery, & Volinsky, 1999). We implemented this procedure using the BIC approximation where models included in the average had ΔBIC < 6 and had no nested submodels with a lower BIC (Raftery, 1995). Bayesian model averaging provides an estimated value (EV) for each parameter, the standard deviation (SD) of the EV, and the posterior probability that the EV is not equal to zero ($P_{\neq 0}$).

We parameterized the full model of DSR to include the landscape variables Core Area and Edge Area, trail width measures WTR and WBH, trail use (GPH), distance from the nest to the nearest trail (TrailDist), the year of the nesting attempt (Year) as a categorical variable, and the number of days since January 1 of the year of nest (OrdDate), as well as the interaction between both measures of trail width and GPH (WTR×GPH, WBH×GPH), the interaction TraiDist×GPH, and the interaction OrdDate×GPH. GPH and the interaction terms that include GPH may provide insight into the effects of direct and indirect disturbance by trail users on nest survival. The variable Year accounts for potential environmental differences among breeding seasons, while OrdDate was included because date of nest initiation within the breeding season is often associated with nest survival (Perrins, 1970). Two study species, Acadian flycatcher and wood thrush, are acceptors of brown-headed cowbird eggs (Evans et al., 2011; Whitehead & Taylor, 2002), so we included information regarding whether a nest was parasitized with the categorical variable ParaStat. American robins are not susceptible to brood parasitism by brown-headed cowbirds (Vanderhoff et al., 2014), so ParaStat was not included in the American robin model. We included the interactions TrailDist×ParaStat, WTR×ParaStat, and WBH×ParaStat because we felt that the distance of a nest from a trail might affect its vulnerability to parasitism and wider trails might increase the chance of a nest being parasitized (Rich et al., 1994). Therefore, our full model for American robin nests contained 8 predictor variables and 4 interaction terms, while the full models for Acadian flycatcher and wood thrush nests contained 9 predictor variables and 7 interaction terms (Appendix 3-2).

3-4 Results

Constructed trails averaged 0.42 GPH (SE 0.14, n = 18), while old road trails averaged 1.23 GPH (0.28, n = 22). Constructed trails had lower use than old road trails (95% highest density interval of the difference (HDI) = (-1.65, -0.16); Figure 3-2a). We found no evidence of human presence in the interior plots. WTR was statistically wider on old road trails (mean width = 2.34 m [SE 0.28], n = 22) than on constructed trails (mean width = 1.11 m [0.11], n = 18; HDI = (-1.87, -0.19); Figure 3-2b), while WBH did not significantly differ between old road trails (mean width = 5.84 m [0.48], n = 22) and constructed trails (mean width = 4.61 m [0.45], n = 18; HDI = (-1.07, 0.25), Figure 3-2c). GPH was linearly related to WTR (Linear regression; β_{WTR} = 0.40 [SE 0.14]; $P < 0.01$; $r^2 = 0.6$; Figure 3-3a), while GPH was not significantly related to WBH ($P > 0.10$; Figure 3-3b). Trail density averaged 1 km/km^2 ([0.15], range: 0.17–2.37 km/km^2, n = 6).

We located 71 Acadian flycatcher nests, and monitored them over 393 exposure periods (Table 3-1). The average exposure period was 3.7 days (SE 0.04; n = 393). Density of Acadian flycatcher nests was not statistically different among plot types within any year (ANOVA, $P > 0.10$; Figure 3-4). We located 81 American robin nests, with 316 exposure periods (Table 3-1). The average exposure period was 4 days ([SE 0.07]; n = 316). Nest density of American robins was significantly different between old road and constructed trails only in 2009 (ANOVA; $P < 0.05$; Figure 3-4). We located 31 Wood thrush nests monitored over 133 exposure periods (Table 3-1). The average exposure period was 3.8 days ([0.09]; n = 133). Wood thrush nest density was significantly higher in plots centered on constructed trails compared to both interior and old road trails in 2012 (ANOVA; $P < 0.05$; Figure 3-4).

The mean distance from nests to the nearest trail was 112 m, 115 m, and 71 m for Acadian flycatcher, wood thrush, and American robin, respectively (Appendix 3-3). There was no difference in distance to constructed versus old road trails for any species. The mean area of core forest within 10 km of nests was 81.5 ha, 74.9 ha, and 75.5 ha for Acadian flycatcher, wood thrush, and American robin, respectively (Figure 3-5a). The area of core forest surrounding nests did not differ with proximity to constructed versus old road trails, for any of the three species (Figure 3-5a). The mean area of forest edge within 500 m of Acadian flycatcher nests, wood thrush nests, and American robin nests was 0.05 ha (SE 0.01); 0.06 ha (0.01), and 0.06 (0.01), respectively (Figure 3-5b). The 500 m radius landscapes surrounding Acadian flycatcher nests contained significantly less edge forest area when the nests were near old road trails than near constructed trails (95% HDI = (-0.08, -0.02); Figure 3-5b). There was no difference in the area of edge forest within 500 m of wood thrush or American robin nests near constructed trails compared to those near old roads (Figure 3-5b).

The average daily survival rate (DSR) of Acadian flycatcher nests (DSR = 0.92; nest success = 0.21) did not differ between trail types ($P > 0.50$). Acadian flycatcher DSR was negatively associated with ordinal date along both trail types in 2012 and 2013 ($\beta_{OrdDate} = -0.98$, $P < 0.01$ and $\beta_{OrdDate} = -2.09$, $P < 0.01$, constructed and old road trails, respectively; Table 3-2) but was not significantly associated with ordinal date in interior forest plots ($P > 0.50$). The average daily survival rate of wood thrush nests (DSR = 0.91; nest success = 0.19) and of American robin nests (DSR = 0.87; nest success = 0.17) did not differ along different trail types (Table 3-2). For these two species the effect of ordinal date on DSR of nests also did not differ according to trail type in 2012 and 2013 (Table 3-2).

Acadian flycatcher nest DSR was negatively related to GPH (BMA: $P_{\neq 0}$ = 1.00; EV_{GPH} = –0.78 [SD 0.19]), the interaction between brood parasitism and WBH (BMA: $P_{\neq 0}$ = 1.00; $EV_{WBH \times PARASTAT}$ = –1.82 [0.45]), the interaction between brood parasitism and WTR (BMA: $P_{\neq 0}$ = 1.00; $EV_{WTR \times PARASTAT}$ = 1.55 [0.45]) and the interaction between GPH and WBH (BMA: $P_{\neq 0}$ = 0.96; $EV_{GPH \times WBH}$ = –1.00 [0.42]; Table 3-3). Wood thrush nest DSR was positively related to the area of core forest within 10 km of a nest (BMA: $P_{\neq 0}$ = 0.66; $EV_{Core\ Area}$: 0.71 [0.67]), and was weakly negatively associated with the interaction between parasitism and the distance from a trail (BMA: $P_{\neq 0}$ = 0.18; $EV_{ParaStat \times TrailDist}$ = –0.20 [0.51]; Table 3-3). American robin nest DSR was weakly positively related to edge area within 500 m (BMA: $P_{\neq 0}$ = 0.21; $EV_{EdgeArea}$ = 0.07 [0.17]) and negatively associated with GPH (BMA: $P_{\neq 0}$ = 0.13; $EV_{EdgeArea}$ = –0.04 [0.14]; Table 3-3).

3-5 Discussion

Our results suggest that both presence of a trail, *per se*, and trail use by hikers adversely affect daily survival rate of two species of passerine in forested protected areas. Both Acadian flycatcher and American robin DSR decreased as the width of the nearest trail and the amount of trail use increased. Wood thrush DSR was positively associated with core forest area as expected, but had an unexpected association with trails, in that DSR decreased with distance to the trail.

Differences in the tread width of the two trail types were not surprising considering their unique structural origins. Road construction creates a compacted path wide enough for vehicle movement, and subsequent conversion to trail use retains this original width characteristic for an extended time as recruitment of woody plants is slowed by soil compaction. On the other hand, modern hiking trail construction practices aim to limit vegetation disturbance (Tennessee Department of & Environment and Conservation, 2007) and the trails are therefore much narrower than old road trails. It was interesting, however, that the mean trail width at 1.4 m above the ground was not significantly different between the trail types. We noticed that on many old road trails exotic honeysuckle (*Lonicera* sp.) had colonized old road edges, which might account for this finding.

Trail use patterns were strongly associated with trail characteristics. Wider trails tended to have higher use. Ten of the 18 old road trail plots in our study were located in Devil's Lake State Park, and had high day use by park visitors, particularly between the end of May and mid-July (Figure 3-1b).

The negative interactive effect of trail width and nest parasitism on DSR of Acadian flycatcher nests may reflect greater success by cowbirds in finding nests in the vicinity of wide trails. Brown-headed cowbirds watch nest building behavior of potential hosts to locate nests (Norman & Robertson, 1975) and wide trails may provide less visual concealment of nest building from brown-headed cowbirds (Burhans, 1997). Our widest old road trails were >10 m, and cowbirds use forest corridors at least as narrow as 8 m (Rich et al., 1994). Old road trails are ubiquitous in protected areas throughout North America, which suggests that such effects are occurring on species throughout protected areas with such trails. In addition to attracting brown-headed cowbirds into interior forests, trails that have a wide vegetation-free zone (WBH), similar to powerline cuts, might provide unobstructed flight paths for nest predators and allow more hunting opportunities in these corridors (Rich et al., 1994).

The DSR of nests for two species, Acadian flycatcher and American robin, was were negatively correlated with the rate of trail use (GPH), as well as trail width. We speculate that the patterns of DSR of Acadian flycatcher and American robins may indicate sensitivity to disturbance by trail users. Regular disturbance from anthropogenic activity is associated with increased corticosterone levels in nesting Great Tits (*Parus major*) and elevated levels of corticosterone are associated with increased brood abandonment (Ouyang et al., 2012; Strasser & Heath, 2013). Our results for Acadian flycatchers and American robins nest DSR may similarly be associated with increased stress hormones and altered time budgets, potentially resulting in decreased incubation time and increased time spent in vigilance behaviors, as has been found in other species

(Smith-Castro & Rodewald, 2010), which can lead to lower DSR (Westmoreland & Best, 1985). Repeated human presence near a nest may also be construed as increased predation risk (Beale & Monaghan, 2004), which is associated with reduced nest attendance and nest investment (Fontaine & Martin, 2006). Understanding the mechanisms responsible for the negative interactive effects is an area of inquiry that is likely to yield critical insights for effectively balancing the breeding habitat function of protected areas with their recreational needs.

Our finding that nest success of wood thrush was lower farther from trails was surprising, as we expected that this species would be sensitive to human disturbance near trails, given their demonstrated sensitivity to forest edges (Weinberg & Roth, 1998). One possible explanation is that since wood thrush forage in leaf litter and semi-bare ground (Evans et al., 2011), they may use the vegetation free spaces of trails or trail edges as foraging areas. We speculate that if ground invertebrate density is higher near trails, perhaps because higher volume of deciduous vegetation due to higher light penetration near trails provides more cover and food for these invertebrates, then selection of nest sites near trails could impart a slight advantage in feeding nestlings and help explain the negative relationship of distance from trail with DSR. A similar result was found for spotted towhees (*Pipilo maculatus*), where juveniles from nests near the park edge were heavier than those in the park interior, possibly because of greater food subsidies near the edge (Shipley, Murphy, & Elzinga, 2013).

Wood thrush DSR was primarily associated with the amount of core forest surrounding nests. This finding supports previous findings that wood thrush nest survival is higher in large tracts than in small forest fragments (Evans et al., 2011; Weinberg & Roth, 1998). We also found American robin DSR was positively related to edge area which is in line with findings that abundance of this species is higher in edge habitats than interior forest in the eastern United States (Best, 2001; King & DeGraaf, 2000; Vora, Leece, & Evers, 2003). The level of forest fragmentation in the Baraboo Hills is similar to that in much of the eastern United States (Riitters et al., 2002), so these findings are broadly interpretable throughout the range of these species.

All three species begin territory establishment between early April (for American robins) and mid-May (wood thrush and Acadian flycatchers) and begin breeding shortly thereafter (Evans et al., 2011; Vanderhoff et al., 2014; Whitehead & Taylor, 2002). High trail use was associated with lower DSR for both American robins and Acadian flycatcher. Old road trails in our study had higher levels of recreational use than constructed trails. Use of all trails greatly increased beginning in the last week of May (Figure 3-1), which follows national trends for National Park recreational use (United States Department of the

Interior, 2015). Acadian flycatcher DSR was lowest along old roads and significantly decreased with ordinal date along both trail types, though the decrease was greater along old road trails than along constructed trails. Wide trails that have low recreational use during the period of territory establishment and early nesting, but heavy recreational use as the breeding season progresses may function as an ecological trap for Acadian flycatchers. Settlement decisions are presumably based on food availability and habitat characteristics (Cody, 1981), and are made before trail use levels reach high levels. Acadian flycatcher DSR was highest in interior plots, where it did not change with ordinal date, possibly due to the lack of human disturbance in interior plots. The patterns of nest density we found suggest that there might be some selection for placing nesting territories close to trails, particularly by Acadian flycatchers and American robins, perhaps because they offer greater foraging opportunities.

3-6 Conclusion

Our study area is characteristic of many protected areas in North America, where public use is supposed to be balanced with resource conservation. However, our findings suggest that the former has negative consequences on the latter. Protected areas often contain some of the most suitable remaining intact habitat for forest-breeding passerines. Our study area contains large tracts of conterminous, low trail density habitat, which may function as population source areas for forest breeding songbirds that are sensitive to fragmentation and recreational disturbance. In low trail density areas (< 0.2 km trail/km^2), given our findings that DSR was lower within 50 m of trails compared to interior forest sites, that less than 2% of the forested area may be affected by recreational use. However, in landscapes without large tracts of trail-less areas, or in protected areas established for the protection of threatened or endangered species, managers may want to consider prioritizing protection over public access during the brief breeding season. We found trail densities in Devil's Lake State Park to be nearly 2.5 km/km^2. If the area within 50 m of trails is of lower quality habitat for some species, as our results suggest, then nearly 25% of the forested area within the park may be sub-optimal nesting habitat. Closing areas of critical breeding habitat to recreational use for the short nesting period, while providing educational information to visitors detailing the rationale, is a strategy that may be warranted in order to ensure continued provision of both breeding habitat and recreational use in protected areas.

3-7 Literature cited

Ballantyne, M., Gudes, O., & Pickering, C. M. (2014). Recreational trails are an important cause of fragmentation in endangered urban forests: A case-study from Australia. *Landscape and Urban Planning*, *130*, 112–124.

Baraboo Range Preservation Association. (2014). Baraboo Range Preservation Association. Retrieved October 14, 2014, from http://baraboorange.org/

Beale, C. M., & Monaghan, P. (2004). Human Disturbance: People as Predation-Free Predators? *Journal of Applied Ecology*, *41*(2), 335–343.

Best, L. B. (2001). Temporal patterns of bird abundance in cornfield edges during the breeding season. *American Midland Naturalist*, *146*(1), 94–104.

Burhans, D. E. (1997). Habitat and Microhabitat Features Associated with Cowbird Parasitism in Two Forest Edge Cowbird Hosts. *The Condor*, *99*(4), 866–872.

Campbell, M. O. (2011). Passerine reactions to human behaviour and vegetation structure in Peterborough, Canada. *Urban Forestry & Urban Greening*, *10*(1), 47–51.

Chan, K. M. A., Shaw, M. R., Cameron, D. R., Underwood, E. C., & Daily, G. C. (2006). Conservation Planning for Ecosystem Services. *PLoS Biol*, *4*(11), e379.

Chapa-Vargas, L., & Robinson, S. K. (2013). Large forests enhance songbird nesting success in agricultural- dominated landscapes of the Midwestern US. *Ecography*, *36*(3), 383–392.

Chapa-Vargas, L., Robinson, S. K., & Johnson, D. H. (2007). Nesting success of acadian flycatchers (empidonax virescens) in floodplain forest corridors. *The Auk*, *124*(4), 1267–1280.

Cody, M. L. (1981). Habitat Selection in Birds: The Roles of Vegetation Structure, Competitors, and Productivity. *BioScience*, *31*(2), 107–113.

Curtis, J. T. (1959). *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press.

Etterson, M. A., Greenberg, R., & Hollenhorst, T. (2014). Landscape and regional context differentially affect nest parasitism and nest predation for Wood Thrush in central Virginia, USA. *The Condor*, *116*(2), 205–214.

Evans, M. L., Gow, E., Roth, R. R., Johnson, M. S., & Underwood, T. J. (2011). Wood Thrush (Hylocichla mustelina). In A. Poole (Ed.), *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology.

Fontaine, J. J., & Martin, T. E. (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters*, *9*(4), 428–434.

Frid, A., & Dill, L. M. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11.

Garrettson, P. R., Richkus, K. D., Rohwer, F. C., & Johnson, W. P. (2010). Factors influencing investigator-caused nest abandonment by North American dabbling ducks. *Canadian Journal of Zoology*, *89*(1), 69–78.

Gates, J. E., & Gysel, L. W. (1978). Avian Nest Dispersion and Fledging Success in Field-Forest Ecotones. *Ecology*, *59*(5), 871–883.

Hesselbarth, W., Vachowski, B., & Davies, M. A. (2007). *Trail Construction and Maintenance Notebook 2007 Edition* (No. 0723-2806-MTDC) (p. 178). United States Department of Agriculture, Forest Service.

Hoeting, J. A., Madigan, D., Raftery, A. E., & Volinsky, C. T. (1999). Bayesian Model Averaging: A Tutorial. *Statistical Science*, *14*(4), 382–401.

Jin, S., Yang, L., Danielson, P., Homer, C., Fry, J., & Xian, G. (2013). A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sensing of Environment*, *132*, 159–175.

Kerbiriou, C., Le Viol, I., Robert, A., Porcher, E., Gourmelon, F., & Julliard, R. (2009). Tourism in protected areas can threaten wild populations: from individual response to population viability of the chough Pyrrhocorax pyrrhocorax. *Journal of Applied Ecology*, *46*(3), 657–665.

King, D. I., & DeGraaf, R. M. (2000). Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. *Forest Ecology and Management*, *129*(1–3), 227–235.

Kruschke, J. K. (2013). Bayesian estimation supersedes the t test. *Journal of Experimental Psychology: General*, *142*(2), 573–603.

Lloyd, P., Martin, T. E., Redmond, R. L., Langner, U., & Hart, M. M. (2005). Linking Demographic Effects of Habitat Fragmentation across Landscapes to Continental Source-Sink Dynamics. *Ecological Applications*, *15*(5), 1504–1514.

Martin, T. E. (1995). Avian Life History Evolution in Relation to Nest Sites, Nest Predation, and Food. *Ecological Monographs*, *65*(1), 101–127.

Martin, T. E., & Geupel, G. R. (1993). Nest-Monitoring Plots: Methods for Locating Nests and Monitoring Success. *Journal of Field Ornithology*, *64*(4), 507–519.

Mayfield, H. (1961). Nesting Success Calculated from Exposure. *The Wilson Bulletin*, *73*(3), 255–261.

Miller, S. G., Knight, R. L., & Miller, C. K. (2001). Wildlife Responses to Pedestrians and Dogs. *Wildlife Society Bulletin*, *29*(1), 124–132.

Neher, D. A., Asmussen, D., & Lovell, S. T. (2013). Roads in northern hardwood forests affect adjacent plant communities and soil chemistry in proportion to the maintained roadside area. *Science of The Total Environment*, *449*, 320–327.

Norman, R. F., & Robertson, R. J. (1975). Nest-Searching Behavior in the Brown-Headed Cowbird. *The Auk*, *92*(3), 610–611.

Outdoor Industry Association. (2012). *the Outdoor Recreation Economy* (p. 20).

Ouyang, J. Q., Quetting, M., & Hau, M. (2012). Corticosterone and brood abandonment in a passerine bird. *Animal Behaviour*, *84*(1), 261–268.

Perrins, C. (1970). The timing of birds' breeding seasons. *Ibis*, *112*(2), 242–255.

Raftery, A. E. (1995). Bayesian model selection in social research. *Sociological Methodology*, *25*, 111–164.

Reed, S. E., & Merenlender, A. M. (2008). Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness. *Conservation Letters*, *1*(3), 146–154.

Rich, A. C., Dobkin, D. S., & Niles, L. J. (1994). Defining Forest Fragmentation by Corridor Width: The Influence of Narrow Forest-Dividing Corridors on Forest-Nesting Birds in Southern New Jersey. *Conservation Biology*, *8*(4), 1109–1121.

Ricklefs, R. E. (1969). *An analysis of nesting mortality in birds.* (Smithsonian Contributions to Zoology No. 9) (p. 56). Washington, DC: Smithsonian Institution.

Riitters, K. H., Wickham, J. D., O'Neill, R. V., Jones, K. B., Smith, E. R., Coulston, J. W., … Smith, J. H. (2002). Fragmentation of Continental United States Forests. *Ecosystems*, *5*(8), 0815–0822.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *The Auk*, *121*(2), 526–540.

Shipley, A. A., Murphy, M. T., & Elzinga, A. H. (2013). Residential edges as ecological traps: postfledging survival of a ground-nesting passerine in a forested urban park. *The Auk*, *130*(3), 501–511.

Smith-Castro, J. R., & Rodewald, A. D. (2010). Behavioral responses of nesting birds to human disturbance along recreational trails. *Journal of Field Ornithology*, *81*(2), 130–138.

Soille, P., & Vogt, P. (2009). Morphological segmentation of binary patterns. *Pattern Recognition Letters*, *30*(4), 456–459.

Strasser, E. H., & Heath, J. A. (2013). Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*, *50*(4), 912–919.

Tennessee Department of, & Environment and Conservation. (2007). *Pathways to Trail Building* (p. 40). Nashville, TN: Tennessee Department of Environment and Conservation.

United States Department of the Interior. (2015). National Park Service Visitor Use Statistics. Retrieved October 23, 2015, from https://irma.nps.gov/Stats/

Vanderhoff, N., Sallabanks, Rex, & James, Frances C. (2014). American Robin (Turdus migratorius). *The Birds of North America Online*.

Verhulst, S., Oosterbeek, K., & Ens, B. J. (2001). Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. *Biological Conservation*, *101*(3), 375–380.

Vogt, P. (2014). GuidosToolbox (Graphical User Interface for the Description of image Objects and their Shapes) (Version 2.1). Retrieved from http://forest.jrc.ec.europa.eu/download/software/guidos

Vora, R. S., Leece, C., & Evers, A. (2003). Songbirds in upland openings and recent clearcuts in northeastern Minnesota. *Loon*, *75*(2), 69–76.

Weinberg, H. J., & Roth, R. R. (1998). Forest area and habitat quality for nesting Wood Thrushes. *The Auk*, 879–889.

Westmoreland, D., & Best, L. B. (1985). The Effect of Disturbance on Mourning Dove Nesting Success. *The Auk*, *102*(4), 774–780.

Whitehead, D. R., & Taylor, T. (2002). Acadian Flycatcher (Empidonax virescens). *The Birds of North America Online*.

Wisconsin Department of Natural Resources. (2015). Devil's Lake State Park. Retrieved March 20, 2015, from http://dnr.wi.gov/topic/parks/name/devilslake/

Zar, J. H. (2010). *Biostatistical Analysis*. Upper Saddle River, New Jersey USA: Prentice Hall.

Zuckerberg, B., & Porter, W. F. (2010). Thresholds in the long-term responses of breeding birds to forest cover and fragmentation. *Biological Conservation*, *143*(4), 952–962.

Table 3-1 Daily survival rate (DSR) of nests of three forest passerine species in protected areas of the Baraboo Hills. Exposure period is the number of times nests were checked, and is presented as average (standard error). Constructed trails minimize forest disturbance by having a narrow tread (< 1 m), following topographic contours, limiting tree removal, and maintaining overhead canopy closure. Old road trails were previously used by vehicles, and have compacted soils, considerable open canopy, and a wide tread (> 2 m).

Species[a]	Constructed trail DSR[b]	Constructed trail nest success[c]	Old road DSR[b]	Old road nest success	Average DSR[b]	Average Nest success
Acadian flycatcher (n = 70)	0.92^{207}	0.222	0.91^{186}	0.214	0.92^{393}	0.222
American robin (n = 81)	0.88^{95}	0.176	0.86^{221}	0.165	0.87^{316}	0.170
wood thrush (n = 31)	0.90^{76}	0.188	0.95^{57}	0.221	0.92^{133}	0.200

[a] n is the total number of nests

[b] The superscript following the DSR estimate is the number of exposure periods for the species

[c] Calculated as (length of nesting period)DSR. length of the nesting period for Acadian flycatcher, wood thrush, and American averages 29, 26, and 26 days, respectively.

Table 3-2 The association between the number of day since January 1 and daily survival rate for three different plot types from 2012 and 2013.

Species	Plot type	DSR[a]	Nest success[b]	$\beta_{OrdDate}$[c]	p
Acadian flycatcher	Interior	0.97 [45]	0.262	-0.22	0.85
	Constructed	0.92 [124]	0.221	-0.98	<0.01
	Old Roads	0.89 [70]	0.200	-2.09	<0.01
wood thrush	Interior	0.85 [13]	0.159	-0.22	0.85
	Constructed	0.80 [10]	0.136	-0.42	0.69
	Old Roads	0.95 [20]	0.221	1.04	0.50
American robin	Interior	0.84 [19]	0.154	-1.88	0.11
	Constructed	0.87 [46]	0.170	0.06	0.84
	Old Roads	0.91 [89]	0.194	0.02	0.97

[a] Superscripts indicate the number of exposure periods.

[b] Calculated as (length of nesting period)^{DSR}. Length of the nesting period for Acadian flycatcher, wood thrush, and American averages 29, 26, and 26 days, respectively.

[c] β in bold indicate significant relationships between DSR and Ordinal Date

Table 3-3 Bayesian model-averaging results for forest passerine nest daily survival rate.

	Acadian flycatcher (N_{models} = 3[a])			wood thrush (N_{models} = 35[a])			American robin (N_{models} = 15[a])		
Parameter	p≠0[b]	EV[c]	SD[d]	p≠0[b]	EV[c]	SD[d]	p≠0[b]	EV[c]	SD[d]
Intercept	100.0	3.93	0.21	100.0	4.09	0.52	100.0	3.29	0.16
OrdDate	21.9	-0.08	0.17	3.2	< 0.01	0.07	2.5	< -0.01	0.02
Year[e]									
2009	0.0			0.0			0.0		
2012	0.0			0.0			0.0		
2013	0.0			0.0			0.0		
CoreArea	0.0			65.7	0.71	0.67	2.7	< 0.01	0.03
EdgeArea	0.0			3.5	0.01	0.08	21.3	0.07	0.17
ParaStat[e]									
Unparasitized (0)	0.0			0.0			---	---	---
Parasitized (1)	0.0			6.0	0.05	0.26	---	---	---
TrailDist	0.0			4.5	-0.01	0.09	3.1	< 0.01	0.04
WBH	0.0			6.9	0.03	0.14	3.3	< -0.01	0.04
WTR	0.0			4.1	-0.01	0.09	3.7	< -0.01	0.04
GPH	100.0	-0.78	0.19	3.1	-0.01	0.07	12.5	-0.04	0.14
ParaStat(1) ×TrailDist	0.0			18.3	-0.20	0.51	---	---	---
ParaStat(1) ×WBH	100.0	-1.82	0.45	2.7	< -0.01	0.07	---	---	---
ParaStat(1) ×WTR	100.0	1.55	0.45	8.1	-0.08	0.33	---	---	---
TrailDist×GPH	0.0			3.3	0.01	0.08	8.9	-0.02	0.10
WTR×GPH	0.0			4.4	-0.01	0.06	2.4	< 0.01	0.03
WBH×GPH	95.9	-1.00	0.42	3.1	-0.01	0.10	8.0	-0.03	0.14
OrdDate×GPH	0.0			9.7	0.05	0.19	4.3	< -0.01	0.06

[a] Nmodels is the number of models used in model averaging.

[b] probability that the estimate value of the parameter is not zero in the model average

[c] estimated value of the parameter

[d] standard deviation of the estimated value

[e] categorical variable, with the categories listed subsequent to the variable name.

3-8 Figure Captions

Figure 3-1 (a) Map of study area in Wisconsin, USA with nest locations, Image from National Agricultural Imagery Program 2012 (United States Department of Agriculture, Farm Services Agency); (b) trail use and first egg date in 2013 in relation to the Memorial Day weekend, the typical time at which visitation to protected areas increases in central Wisconsin.

Figure 3-2 Boxplots of (a) groups per hour (GPH), (b) tread width (WTR) in meters, and (c) width at 1.4 m from the ground (WBH), in meters, for constructed and old road trails. For each pair, stippled boxes indicate the group with significantly higher mean. The 95% highest density interval (HDI) indicates the difference in means from Bayesian estimation and is shown as a black bar on the bottom plot.

Figure 3-3 Relationship between trail use and trail width. Linear regression between groups per hour and tread width (WTR). Gray area indicates the 95% confidence interval.

Figure 3-4 Nest density, by year for Acadian flycatchers, wood thrush, and American robin. Different letters above bars indicate significant differences (ANOVA; $P < 0.05$) in nest density between plot types within a year. There were no interior plots in 2009.

Figure 3-5 Boxplots for the areas of (a) core forest within 10 km and (b) edge forest area within 500 m of Acadian flycatcher, wood thrush, and American robin nests. For each species, stippled boxes indicate the group with significantly higher mean. The 95% highest density interval (HDI) indicates the difference in means from Bayesian estimation and is shown as a black bar on the bottom plot.

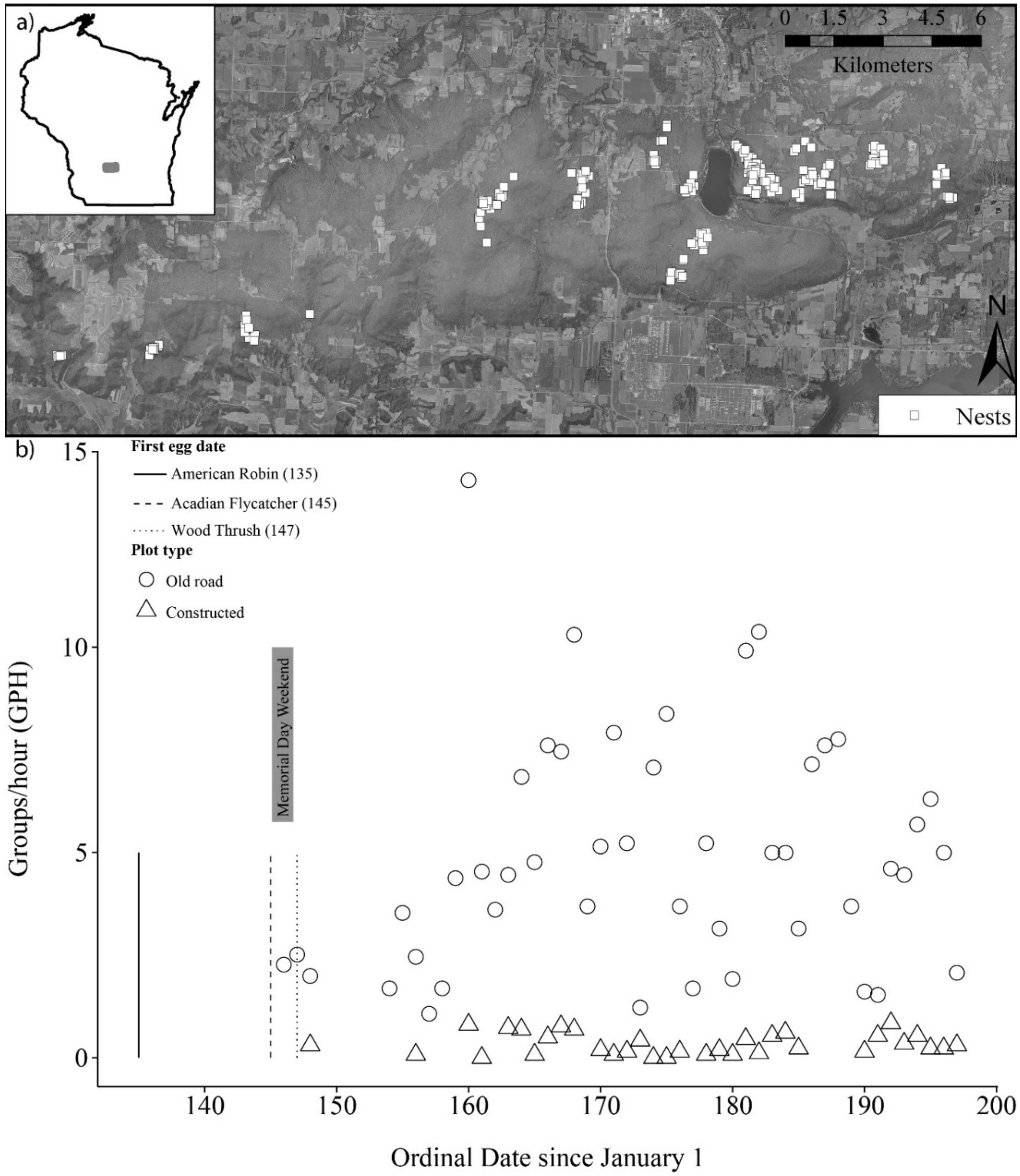

a)
0 1.5 3 4.5 6
Kilometers
N
Nests
b)
First egg date
American Robin (135)
Acadian Flycatcher (145)
Wood Thrush (147)
Plot type
Old road
Constructed
Memorial Day Weekend
Groups/hour (GPH)
Ordinal Date since January 1
0
5
10
15
140
150
160
170
180
190
200

Figure 3-1

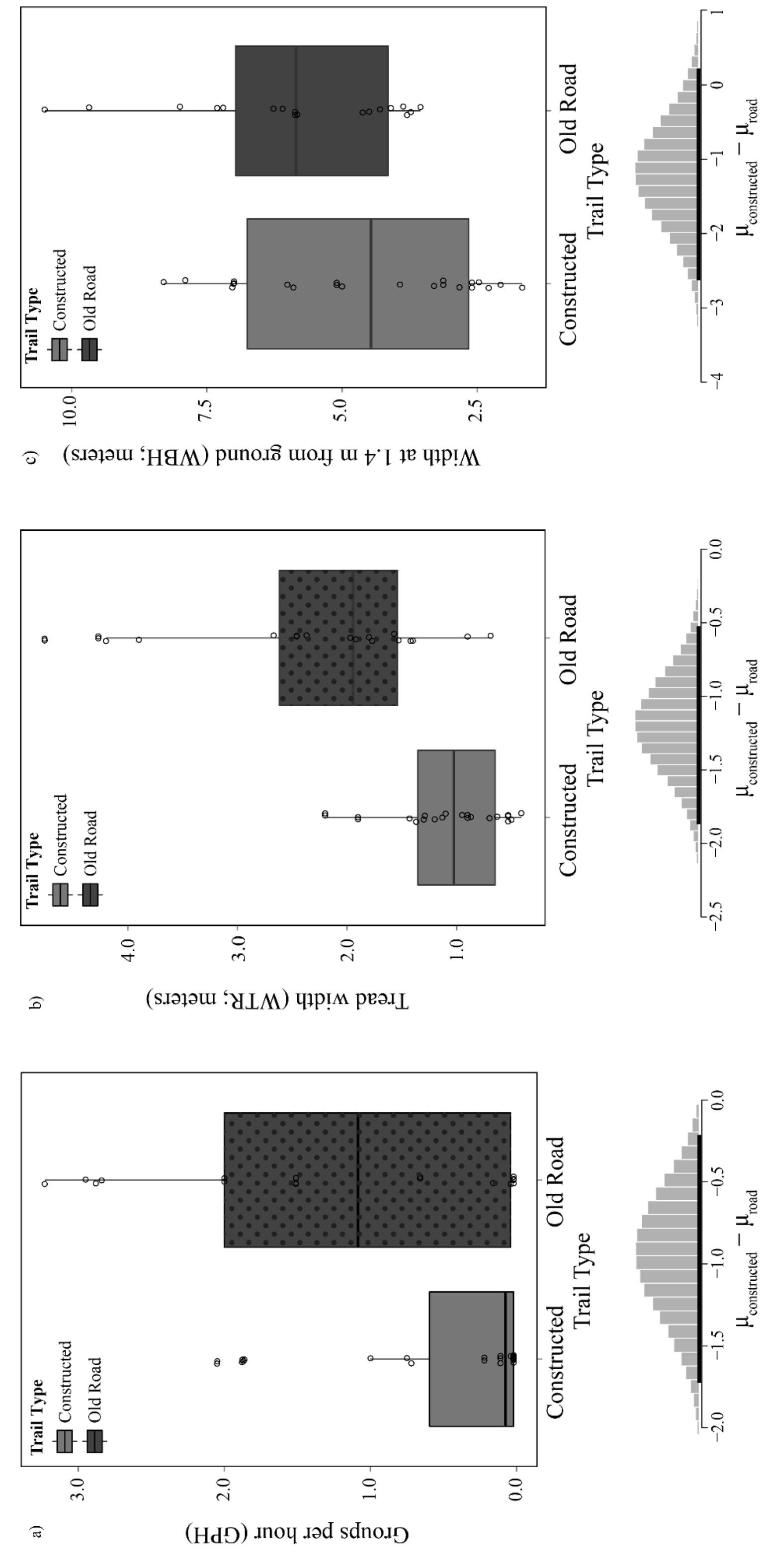

a)
Groups per hour (GPH)
Trail Type
Constructed
Old Road
Constructed
Old Road
Trail Type
b)
Tread width (WTR; meters)
Trail Type
Constructed
Old Road
Constructed
Old Road
Trail Type
c)
Width at 1.4 m from ground (WBH; meters)
Trail Type
Constructed
Old Road
Constructed
Old Road
Trail Type
$\mu_{constructed} - \mu_{road}$
$\mu_{constructed} - \mu_{road}$
$\mu_{constructed} - \mu_{road}$

Figure 3-2

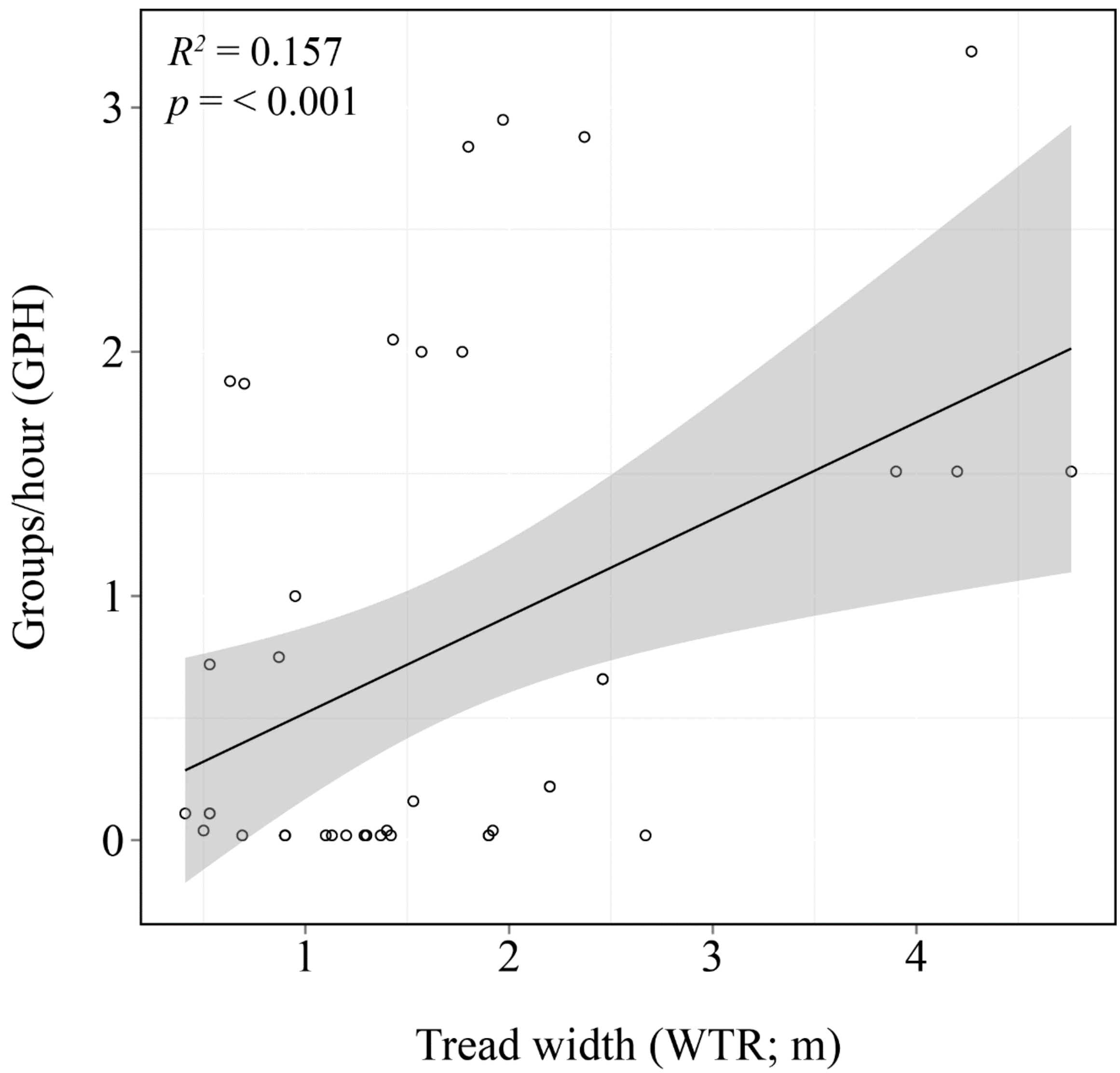


Figure 3-3

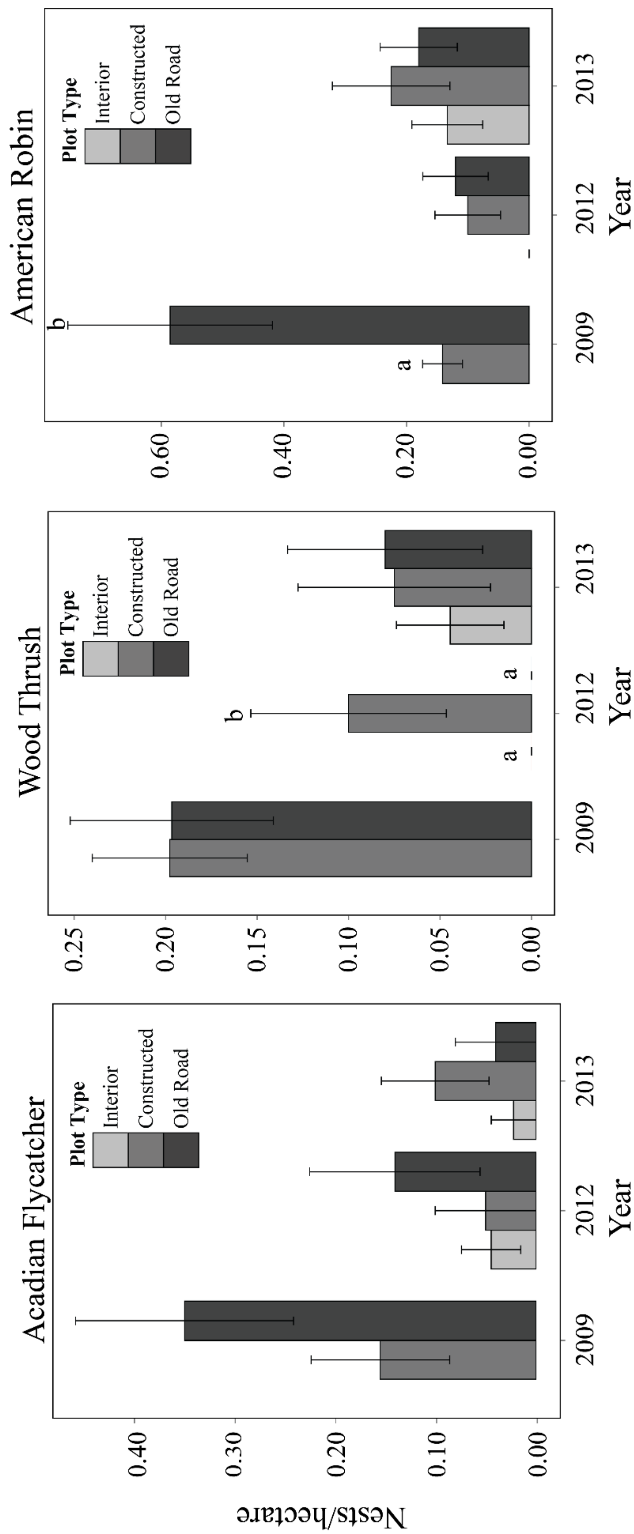

Acadian Flycatcher
Wood Thrush
American Robin
Plot Type
Interior
Constructed
Old Road
Nests/hectare
Year
2009
2012
2013
a
b

Figure 3-4

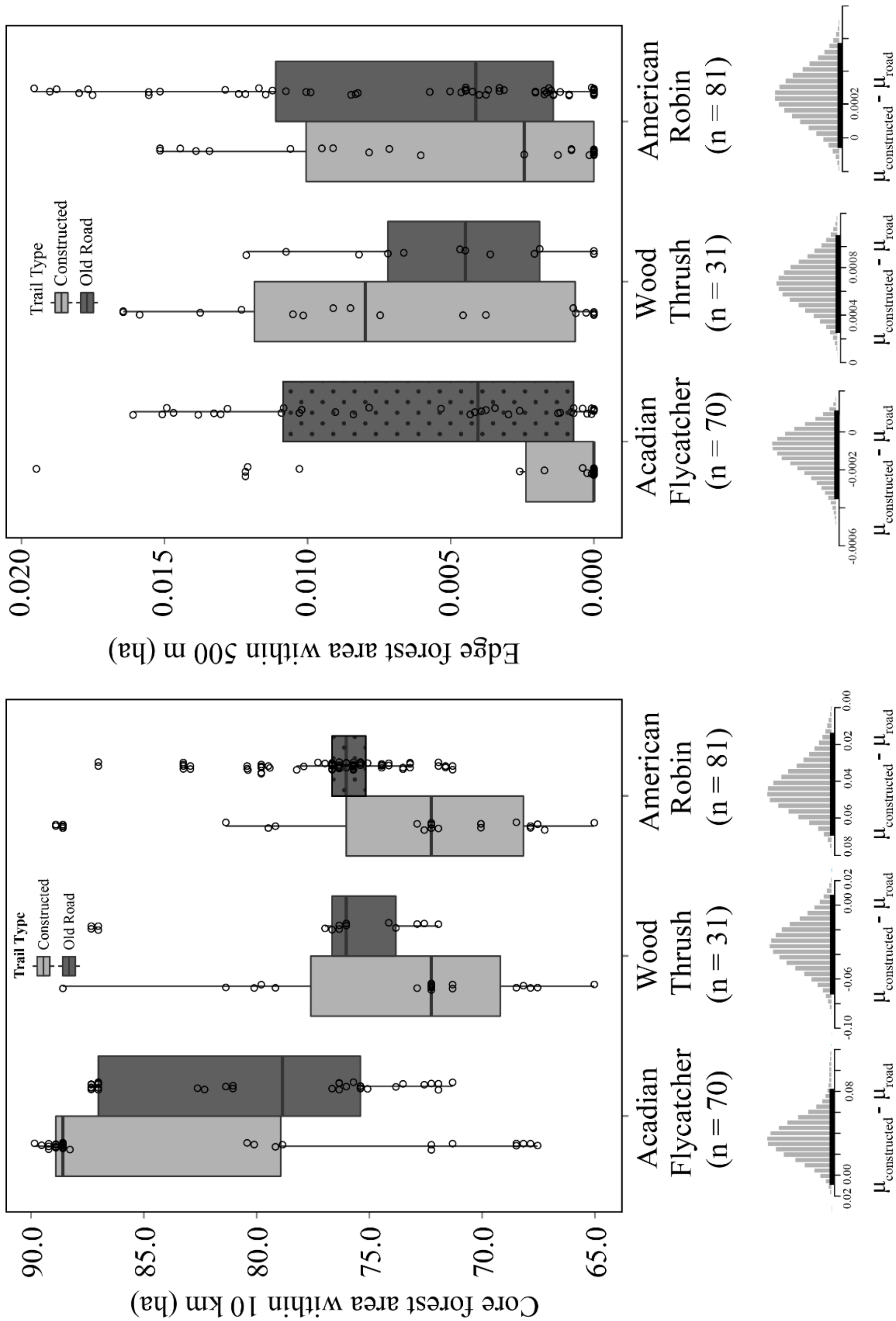

Core forest area within 10 km (ha)
Edge forest area within 500 m (ha)
Trail Type
Constructed
Old Road
Acadian Flycatcher (n = 70)
Wood Thrush (n = 31)
American Robin (n = 81)
μconstructed - μroad

Figure 3-5

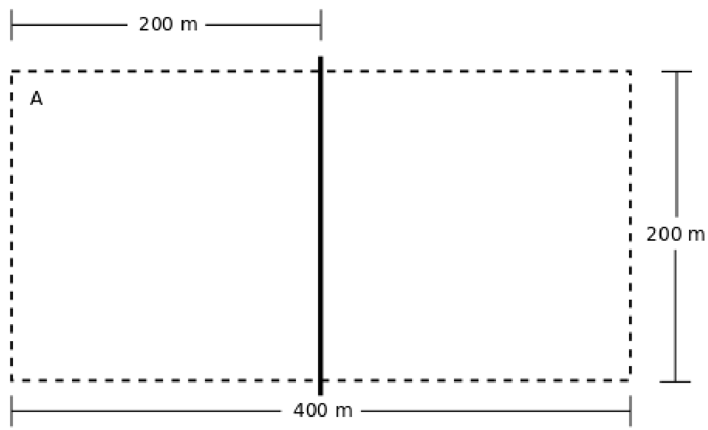
3-9 Appendices

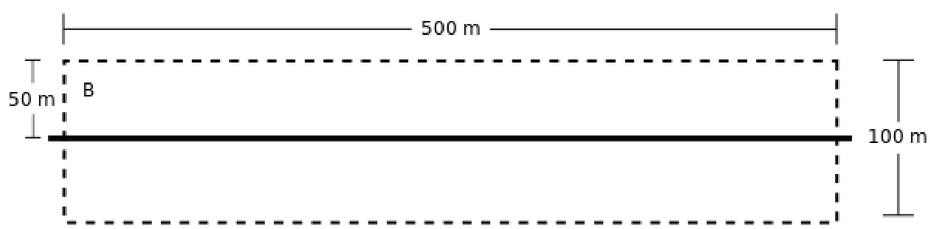
Appendix 3-1 Study plot design. (A) Study plots in 2009 were 400 m wide and 200 m long, bisected by a trail. (B) Study plots in 2012-2013 were 100 m long and 500 m wide, bisected by a trail. Trails are indicated by the solid line.

Appendix 3-2 Description of logistic exposure regression model variables used in forest passerine daily survival rate logistic exposure models.

Appendix 3-3 Boxplots for the distance from nests to the nearest trail of Acadian Flycatchers, Wood Thrush, and American Robins. The 95% highest density interval (HDI) of the difference in means is indicated as a black bar on the bottom plot.

Appendix 3-1

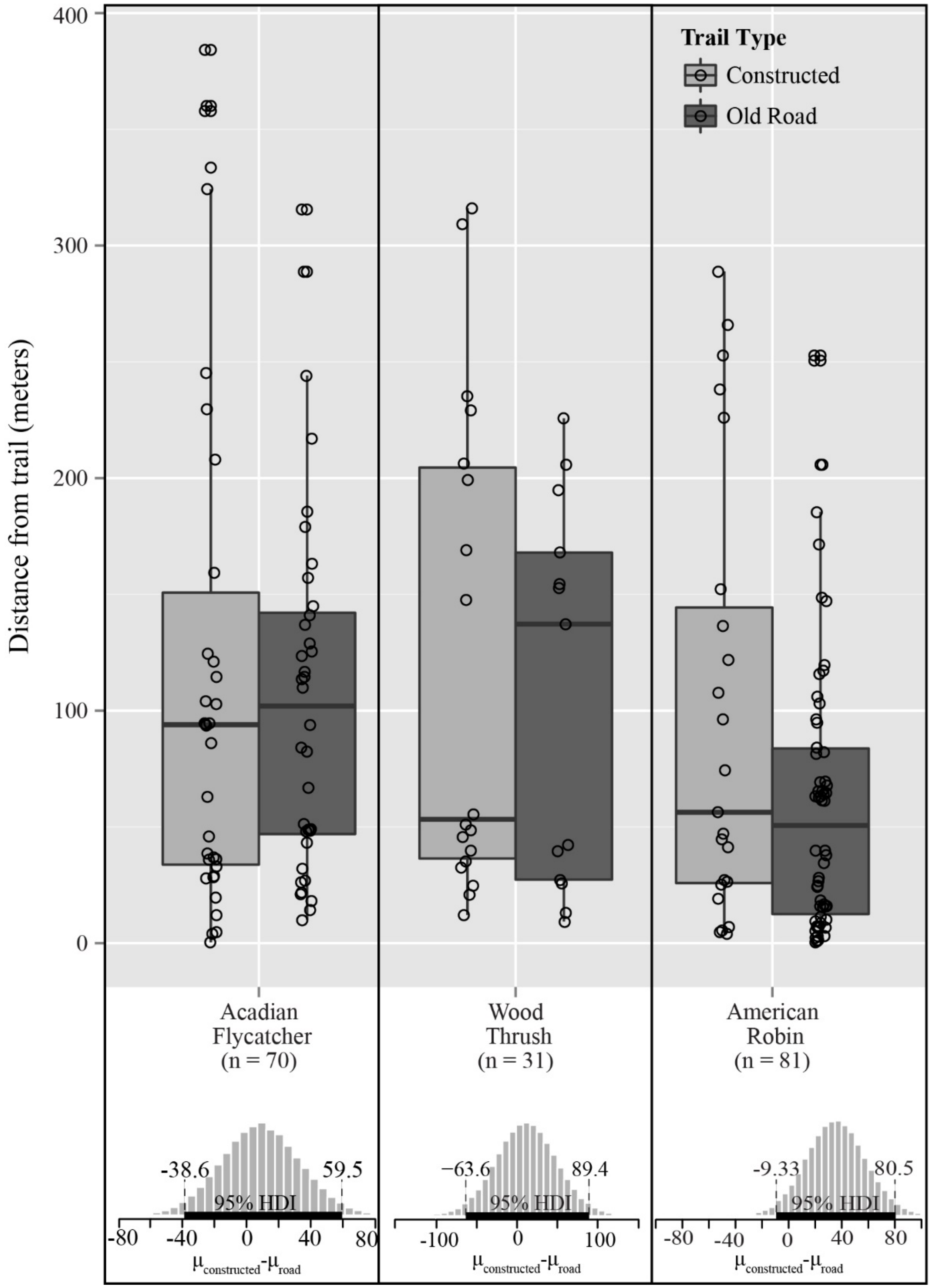




Appendix 3-2

Variable	Description
OrdDate	Ordinal date since January 1 of the year of nest attempt
Year	Year nest was observed
Edge Area	Amount of 60 m forest edge within 500 m of nest
Core Area	Amount of non-edge forested area within 10 km of nest
TrailDist	Distance from the nest to the nearest trail
WTR	width of tread for the nearest trails
WBH	width of trail opening at 1.4 m from trail surface
GPH	groups of trail users per hour
GPH×TrailDist	Interaction between GPH and TrailDist
GPH×WTR	Interaction between GPH and WTR
GPH×WBH	Interaction between GPH and WBH
GPH×OrdDate	Interaction between GPH and OrdDate
ParaStat†	Brood parasitism status (0 = unparasitized; 1 = parasitized)
Parasitized×TrailDist†	Interaction between category parasitized and TrailDist
Parasitized×WTR†	Interaction between category parasitized and WTR
Parasitized×WBH†	Interaction between category parasitized and WBH

Appendix 3-3


Trail Type
Constructed
Old Road
400
300
200
100
0
Distance from trail (meters)
Acadian Flycatcher (n = 70)
Wood Thrush (n = 31)
American Robin (n = 81)
-38.6
59.5
95% HDI
-80
-40
0
40
80
−63.6
89.4
-100
100
-9.33
80.5
μconstructed-μroad