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George Todd & Zachary Stahlschmidt

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Effects of habitat features and season on vertebrate communities in Southern Georgia, U.S.A

George Todd^{a,b} and Zachary Stahlschmidt^{a,c}

^aBiology Department, Georgia Southern University, Statesboro, GA, USA; ^bGeneral Education Department, Coastal Pines Technical College, Waycross, GA, USA; ^cBiological Sciences Department, University of the Pacific, Stockton, CA, USA

ABSTRACT

Although the southeastern U.S.A. contains a high diversity of species and habitats, this region is also experiencing rapid human development. Humans are modifying ecosystems in complex ways, and these changes often result in shifts in biodiversity. Therefore, examining habitat use in human-altered ecosystems gives insight into how animals will continue to respond to their rapidly changing environments. Biodiversity and abundance can be influenced by several factors, including habitat structure and seasonal variation. Understanding how these factors influence biodiversity is particularly important in areas that are experiencing high levels of human activity. Thus, we surveyed artificial cover objects to examine the effects of forest structure and season on several indices of diversity in vertebrates (mammals, reptiles, and amphibians) in forested sites in the southeastern U.S.A., a region characterised by rapid human population growth. Vertebrate abundance varied by season where abundance in the fall and winter were lower than in the spring and summer. The proximity to roads affected vertebrate abundance where abundance was higher under cover objects farther from roads. Our results provide evidence that anthropogenic, biotic, and temporal factors can influence vertebrate abundance and biodiversity. We also provide insight into the role of forest structure in vertebrate biodiversity, and we encourage future efforts focusing on the role of structural variation across different ecosystems.

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Introduction

The southeastern U.S.A. exhibits high biodiversity (Stein 2002) and contains species that inhabit a wide range of habitats, including several types of forest (e.g. mangrove, oak-hickory, bottomland, and pine) (Parks 2013; Stein 2002; White and Wilds 1998). In addition to harbouring many plant and animal species, this region is also increasingly the home of humans: the Southeast was the fastest growing region in the U.S.A. from 2000 to 2010 (Mackun and Wilson 2011). Humans are modifying ecosystems in complex ways, and these changes often result in observed changes in the biodiversity (Buczowski and Richmond 2012; Travis 2003) and distribution of animal species (Ordiz et al. 2014; Pike, Webb, and Shine 2011; Sato et al. 2014). Anthropogenic modifications of the landscape often take the form of habitat loss and fragmentation, which can affect animal behaviour (Knopff et al. 2014) and greatly threaten species abundance (Zamfirescu et al. 2011). Therefore, examining habitat use in human-altered ecosystems provides insight into how animals will continue to respond to their rapidly changing environments (Kloskowski, Rechulicz, and Jarzynowa 2013; Pham et al. 2014; Vandevelde et al. 2014).

Forests are a priority in studying human-habitat interactions because they provide habitat for more than half the world's terrestrial species (Groombridge and Jenkins 2000) and host numerous vulnerable species (Jenkins et al. 2015). The influence of human activity on forest ecosystems has been well articulated (Cornulier and Bretagnolle 2005; Meijaard and Sheil 2008; Peters, Malcolm, and Zimmerman 2006, but see Blood et al. 2016). Specifically, human activity can cause changes in landscape structure (Faulkner 2004; Nagy and Lockaby 2010), including changes in patch size (Kapos, Lysenko, and Lesslie 2000), canopy cover (Blouin-Demers and Weatherhead 2001), and edge density (Blouin-Demers and Weatherhead 2001). Although such factors have been studied broadly across forest ecosystems, their role in forests in the southeastern U.S. is less studied and deserves attention (Loeb, Post, and Hall 2009; Nagy & Lockaby 2010; Blood et al. 2016). Because the diversity of animal taxa can be influenced by habitat features (e.g. composition of forest: Mazurek and Zielinski 2004), it is important to account for a range of structural variables related to habitat (e.g. canopy cover, distance to edges, etc.) when studying human-impacted forests.

Several metrics of biodiversity may also vary seasonally (Grøtan et al. 2012; Liu et al. 2013; Shimadzu et al. 2013). Seasonal changes heavily influence species in several ways – from the life history stages of insects to the migratory patterns of birds (Rosenzweig 1995). Climate change can amplify seasonal effects, which may threaten forest-dependent species (Thomas et al. 2004). Further, surveys of biodiversity depend on biologists' ability to observe species in their habitats, and it can be difficult to obtain accurate data as many taxa alter their activity based on the seasons (Houze and Chandler 2002; Paul, Zucker, and Schwartz 2008; Rizkalla et al. 2015). Thus, it is important to account for seasonal variation when examining biodiversity (e.g. Brotherton, Behler, and Cook 2007; Houze and Chandler 2002; MacNeil and Williams 2014).

Therefore, we examined the effects of forest structure and season on several indices of biodiversity to test two hypotheses in forested sites in the southeastern U.S. A. that reflected the range of management practices and proximity to human development indicative of the region. First, we hypothesised that landscape structure would influence the abundance of vertebrate taxa (mammals, reptiles, and amphibians). Although several habitat variables may influence vertebrate abundance patterns (e.g. canopy cover or proximity to roads), we specifically predicted that the distance to the nearest edge (a border between habitat types, such as the border between a forest and a habitat consisting of short vegetation) would be the strongest indicator of such patterns because of edges' importance in thermoregulation and foraging in other forest systems (e.g. Blouin-Demers and Weatherhead 2001; reviewed in Laurance 2008). Second, we hypothesised that vertebrate diversity would be affected by season, and we specifically predicted that biodiversity indices would be higher during the more mild spring and fall months when vertebrates display more above-ground activity (Bakkegard 2002; Brito 2003; Foá et al. 1994; Stahlschmidt, Walman, and Mills 2018). The results of our study will give insight into the factors driving vertebrate diversity in a forest ecosystem in a region undergoing rapid growth in the human population (Mackun and Wilson 2011).

Materials and methods

Study areas and sampling

We carried out this study from September 2014 to September 2015 and used five forested sites across two locations in the sub-tropical climate of southeast Georgia (GA), U.S.A. Each site varied in land-management practice, as well as proximity to human development. One

location was near Metter, GA, and contained three sites with different types of rural forests: sand hill (M-SH), mature pine (M-MP), and immature (3–4 years old) long-leaf pine (M-IP). The distances between the sites ranged from 0.6 to 0.8 km. The second location was 24 km east of the Metter location and adjacent to human development in Statesboro, GA, a city with a population of approximately 30,000 residents (U.S. Census Bureau) surrounded by forest and agriculture. It contained two sites: mature pine with a modified sand hill on the campus of Georgia Southern University (S-GS) and a bottomland forest that abuts residential housing (S-RH). The distance between the two sites was 0.6 km.

We established each of the five sites with an array of 20–25 cover boards (minimum convex polygons of arrays: 2.3–4.6 hectares), which were artificial cover objects consisting of two pieces of corrugated steel sheeting (1 m × 1.5 m) laid on the ground on top of each other (*sensu* Joppa 2009; Stahlschmidt, Walman, and Mills 2018). Cover boards are an effective way of measuring vertebrate diversity (e.g. Costall and Death 2010; Grant et al. 1992; Houze and Chandler 2002; MacNeil and Williams 2014). Approximately twice per month, we overturned each cover board to document the presence of vertebrate genera, as well as ant colonies. Ants can influence vertebrate behaviour, such as foraging (Orrock and Danielson 2004) and predator avoidance (Langkilde 2010; Long et al. 2015), and colonies of ants (*Camponotus floridanus*, *C. pennsylvanicus*, and *Solenopsis invicta* in our study) use artificial cover objects and are easy to observe. For vertebrates, we calculated richness (R, the number of taxa present), Shannon's Diversity (H), and Shannon's Evenness (E) for each site during each season because R, H, and E are effective metrics for estimating biodiversity (Magurran 2004). We compared metrics of vertebrate abundance and diversity across meteorological seasons (i.e. spring: March–May; summer: June–August; fall: September–November; winter: December–February).

Habitat characterization

To characterise the structural features of the forested sites, we measured several abiotic and biotic variables. We used several structural variables to characterise the habitats at each site (patch size) or near each cover board (all other variables: see below). Patch size, or an area of habitat surrounded by a border that constitutes a change in habitat type, can play an integral role in ecosystem dynamics (Pickett and White 1986). We measured patch size at each site via Garmin GIS devices and software (BaseCamp, v.4.6.2). Canopy cover, a measure of the degree to which foliage blocks sunlight from reaching

the ground in a forest habitat, is a key variable when characterizing the thermal quality of habitats (Blouin-Demers and Weatherhead 2001). We measured canopy cover during the summer (July 2015) to estimate the maximum yearly value at each cover board. We determined canopy cover at each cover board by measuring photographs taken through a fisheye lens using ImageJ software (version 1.48, National Institute of Health). We measured the distance to the nearest snag (tree stump or log ≥ 7.5 cm), overstory tree, road (d-road), and building (modified from Blouin-Demers and Weatherhead 2001). Although road density has been shown to affect vertebrate abundance (Fahrig and Rytwinski 2009), we instead determined d-road because the presence of multiple roads within 100 m of cover boards was rare in our study. We also measured the distance to the nearest edge. Edges can be natural or anthropogenic (e.g. created via mowing, burning, or other land practices) and are key to understanding thermoregulation because they represent a distinct shift in thermal characteristics within a habitat (Blouin-Demers and Weatherhead 2001).

We square root transformed all abundance values gathered from the sites and performed non metric multidimensional scaling (NMDS) to ordinate the data and visualise resemblance patterns by site and season – that is, NMDS allowed visualisation of the effects of site and season on vertebrate abundance (see below).

Statistical analyses

We performed analyses in SPSS (v.22 IBM Corp., Armonk, NY) and Primer 7 (v.7.0.8 Lutton, UK). When necessary, we either square root transformed or logarithmically transformed data to achieve normality. We determined two-tailed significance at $\alpha < 0.05$.

We used a distance-based linear model (an extension of a traditional linear model: Boj et al. 2015) to determine relationships between abundance values and habitat variables (i.e. to address our first hypothesis that habitat variables influence vertebrate abundance). Our distance-based linear model used the ordinary cross-validation estimate of the prediction error (ocv) method (a step-wise approach). The season was included as a fixed effect, site as a random effect, and the habitat variables as covariates.

We also performed several tests to examine if vertebrate diversity varied due to the location (i.e. Metter, GA vs. Statesboro, GA) and season. Due to a relatively low-observed abundance of vertebrates, we also analysed observation data that were pooled by season (e.g. for spring: the sum of all individuals observed under cover boards from March to May 2015). To test for differences in abundance due to the fixed effects of site and season, we used

a permutational analysis of variance with pair-wise tests. Then, we square root transformed all abundance values gathered from the sites and performed non metric multidimensional scaling (NMDS) to ordinate the data and visualise resemblance patterns by site and season – that is, NMDS allowed visualisation of the effects of site and season on vertebrate abundance. To determine seasonal effects on R, H, and E of all vertebrate classes and genera, we next used linear mixed models on all vertebrate genera and the genera for each taxon (i.e. to address our second hypothesis that season-influenced biodiversity). We included season as a fixed effect, the percentage of observations of ants as a covariate, site as a random effect, and diversity indices as dependent variables. Due to limited sample size (e.g. only two genera of mammals were observed during the study), we did not analyse E in amphibians or mammals, nor did we analyse H in mammals.

Results

A total of 3 classes, 16 genera and 20 species were observed under cover boards over the course of the study (Table 1).

Vertebrate abundance varied by season where fall/winter and spring/summer were the only season combinations that were similar to one another (Table 2). Note the points in Figure 1 are clustered between spring/summer and fall/winter on the left and right sides, respectively. There was also significant spatial autocorrelation because vertebrate abundance differed between sites M-SH and S-RH ($F_{4,19} = 3.5$, $P = 0.04$), M-MP and S-RH ($F_{4,19} = 3.5$, $P = 0.05$), and M-IP and S-RH ($F_{4,19} = 3.5$, $P = 0.04$) (Figure 1). Note the points in Figure 1 also show that Site S-RH differed from all three Metter sites. The points for all

Table 1. Observed abundance of species found across seasons at five forested sites in southern Georgia, U.S.A. Genera with more than one species observed are denoted with an * (*Ambystoma opacum*, *talpoideum*, *Bufo quercicus*, *terrestris*, *Eumeces fasciatus*, *inexpectatus*, *laticeps*).

Class	Genera	Season			
		Spring	Summer	Fall	Winter
Amphibia	<i>Ambystoma</i> *	8	1	7	7
	<i>Bufo</i> *	3	5	0	3
	<i>Gastrophryne carolinensis</i>	4	0	0	0
	<i>Lithobates sphenoccephalus</i>	3	1	7	10
Reptilia	<i>Anolis carolinensis</i>	8	2	52	62
	<i>Aspidoscelis sexlineatus</i>	9	0	0	1
	<i>Coluber constrictor</i>	7	11	1	1
	<i>Diadophis punctatus</i>	3	3	1	4
	<i>Eumeces</i> *	69	37	0	0
	<i>Lampropeltis getula</i>	1	1	0	1
	<i>Masticophis flagellum</i>	2	1	2	1
	<i>Nerodia fasciata</i>	2	0	0	1
	<i>Ophisaurus ventralis</i>	2	0	1	0
	<i>Scincella lateralis</i>	0	3	28	19
Mammalia	<i>Blarina carolinensis</i>	1	0	0	2
	<i>Peromyscus gossypinus</i>	0	0	26	34

Table 2. Effects of season (spring, summer, fall, and winter) and site (Metter sand hill [M-SH], Metter mature pine [M-MP], Metter immature, longleaf pine [M-IP], Statesboro residential housing [S-RH], and Statesboro campus of Georgia Southern University [S-GS]) on the abundance of all observed vertebrates at five forested sites in southern Georgia, U.S.A. based on permutational analyses of variance with pair-wise tests. See text for details about sites, and see Figure 1 for a visualisation of these results.

		t	P
Season	Fall, Winter	0.71	0.68
	Fall, Spring	3.0	0.01
	Fall, Summer	3.1	0.01
	Winter, Spring	3.1	0.01
	Winter, Summer	3.7	0.02
	Spring, Summer	1.5	0.10
Site	M-SH, M-MP	1.5	0.16
	M-SH, M-IP	1.4	0.20
	M-SH, S-RH	3.4	0.04
	M-SH, S-GS	2.2	0.07
	M-MP, M-IP	1.4	0.23
	M-MP, S-RH	2.1	0.05
	M-MP, S-GS	1.5	0.18
	M-IP, S-RH	2.5	0.04
	M-IP, S-GS	1.7	0.11
	S-RH, S-GS	1.4	0.14

four seasons of the S-RH are clustered at the top of the figure whereas the points for the Metter sites, although split by seasonal differences, are located closer to the bottom of the figure. The stress value (the degree to which the data is represented by the dimensions in the plot) for Figure 1 (0.12) is acceptable for an NMDS ordination (Buttigieg and Ramette 2014).

Season influenced H of all vertebrate classes where H for all vertebrates was greater in the summer than in

the fall and winter (sequential Bonferroni-adjusted pair-wise comparison) (Figure 2; Table 3). The percentage of cover boards occupied by ants positively covaried with the H of all vertebrate classes and the E of reptile genera (Table 3). Neither the presence of ants nor season were significantly associated with other metrics of biodiversity for all vertebrate classes, all vertebrate genera, or the genera for each taxon (Table 3).

The distance-based linear model explained 28% of the total variance invertebrate abundance. D-road significantly influenced vertebrate abundance where a higher number of vertebrates were observed under cover boards far from roads (Table 4). No other habitat variables influenced vertebrate abundance (Table 4).

Discussion

Vertebrate abundance was influenced by the d-road, which partially supported our first hypothesis that landscape structure would influence vertebrate abundance (Figure 1). Season influenced H of classes (Figure 2) where H was greater in the summer than in the fall and winter. Yet, we predicted higher biodiversity in the milder spring and fall seasons for our second hypothesis that vertebrate diversity would be affected by season. Together, these results demonstrate that season and habitat structure influenced vertebrate biodiversity in our study system. D-road was the only structural variable that influenced vertebrate abundance where abundance was inversely related to d-road. This result is relevant to ‘road-ecology’, which has gained attention

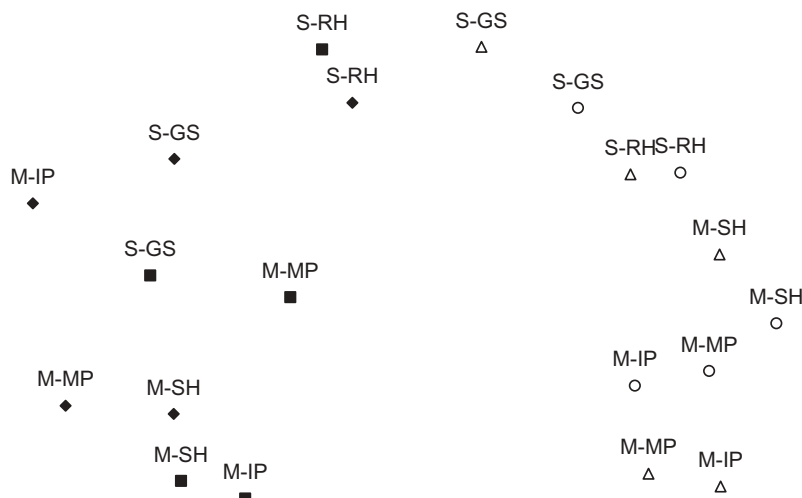


Figure 1. Nonmetric multidimensional scaling ordination plot based on the relative abundance of vertebrates observed across all seasons in five forested sites in southeastern Georgia, U.S.A. . Distances between sample points represent differences based on Bray-Curtis dissimilarity (e.g. symbols that cluster close to one another exhibited similar levels of vertebrate abundance; Bray and Curtis 1957). Triangles represent fall, circles: winter, squares: spring, diamonds: summer. Black symbols represent spring and summer seasons, and white symbols represent fall and winter seasons. Sites are as follows: M-SH, M-MP, and M-IP (for sand hill, mature pine, and immature pine sites near Metter, GA), and S-GS and S-RH (for Georgia Southern University and residential housing sites in Statesboro, GA).

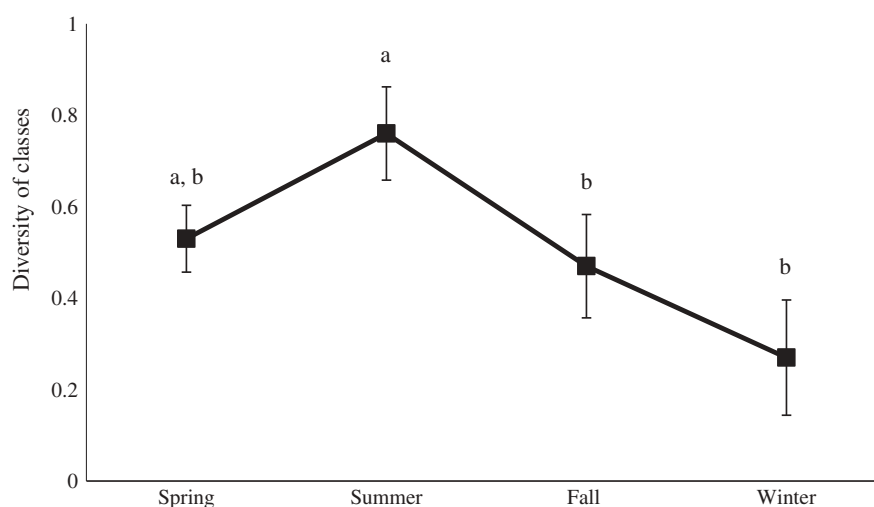


Figure 2. Effect of season on Shannon's index of diversity (H) of vertebrate classes in forests in southeastern Georgia, U.S.A. Shared letters above points represent non-significant ($p > 0.05$) differences between seasons. Symbols represent mean ± 1 SE.

as the network of roads in the U.S.A. continues to rapidly expand (Fahrig and Rytwinski 2009). This is evidenced by the creation of the International Conference on Ecology and Transportation, as well as various road-ecology research centres. However, not all roads are created equally, and we encountered paved and unpaved roads at our sites. Unpaved roads may impact wildlife less than paved roads because they experience less disturbance and traffic (Andrews, Nanjappa, and Riley 2015). Yet, unpaved roads are not without costs to ecosystems as they are more vulnerable to erosion, can smother surrounding streams and vegetation, and generate significant dust during dry periods (Strayer 2012). Roads often have negative effects on animal populations for several reasons, including direct mortality risk (Forman et al. 2003) and reduced accessibility to habitat and resources (Jaeger and Fahrig 2004). However, some species can experience neutral or positive road effects. Typically, these species are either (1) attracted to roads for food and can avoid mortality (e.g. vultures) or (2) avoid road contact but are not disturbed by traffic and easily avoid traffic (e.g. small mammals and birds) (Fahrig and Rytwinski 2009). The inverse relationship between vertebrate abundance and d-road that we found aligns with previous work demonstrating the susceptibility of herpetofauna to roads (Fahrig and Rytwinski 2009) given 86% of our observations were of amphibians and reptiles (Table 1).

The effects of roads on animal habitat use is made complex by the fact that, although roads can fragment a landscape, they can also increase the number of edges in a landscape (Mehmood and Zhang 2001; Murcia 1995). Ecological edges separate habitats and can be ecologically advantageous because they allow quick movement to

adjacent habitats and facilitate thermoregulation (Blouin-Demers and Weatherhead 2002; Murcia 1995; but see Hanski, Fenske, and Niemi 1996; Kingston and Morris 2000). Despite these advantages for certain taxa, edges can be a double-edged sword as they can also allow easy access to habitats by predators, cause higher rates of nest predation, and parasitism (birds: Gates and Gysel 1978). Although we found no support for our prediction that proximity to edge would drive abundance, edge effects are dynamic and can vary in time and space (Laurence et al. 2007). One possible explanation for our negative result related to edge effects is that edge effects have been found to increase with habitat area (Ewers, Thorpe, and Didham 2007), and our sites were relatively small (<14 hectares). Edge effects also tend to be greater when a forest edge borders agricultural or pastureland as opposed to another forest patch (Mesquita, Delamônica, and Laurance 1999). However, all five of our sites had at least some edges adjacent to more forest patches. Although we did not find edge effects in our study, future studies should continue to account for edge density as it can have a significant influence on biodiversity (Laurence et al. 2007; Saunders, Hobbs, and Margules 1991).

In contrast to our second prediction (higher diversity in the milder spring and fall seasons) and other work in forests in southeastern U.S. (Stahlschmidt, Walman, and Mills 2018), H in our study was greater in the summer than in the fall and winter (Figure 2). This effect may be attributed to the seasonal activity patterns of the taxa observed in our study – most of the taxa (i.e. ectotherms) are largely inactive and fossorial during cooler months (Halliday 1994; Ultsch 1989). Beyond this generalisation, understanding the biology of our commonly encountered taxa (Table 1) may provide insight into shifts in observed

Table 3. Effects of seasonality and the presence of ants on the richness, Shannon's diversity, and Shannon's evenness of all observed vertebrates and each vertebrate taxon at five forested sites in southern Georgia, U.S.A. based on linear-mixed models. Due to limited sample size (e.g. only two genera of mammals were observed during the study), evenness was not analysed in amphibians or mammals, nor was Shannon's diversity analysed in mammals.

	F	P
Vertebrata		
Class Richness		
Season	2.4	0.12
Ants	0.36	0.56
Class Shannons' Diversity		
Season	5	0.016
Ants	5.6	0.039
Class Shannons' Evenness		
Season	2.5	0.11
Ants	4.1	0.063
Genera Richness		
Season	1.4	0.28
Ants	0.29	0.61
Genera Shannons' Diversity		
Season	1.1	0.39
Ants	0.005	0.94
Genera Shannons' Evenness		
Season	0.44	0.73
Ants	0.002	0.97
Amphibia		
Richness		
Season	1.1	0.4
Ants	0.044	0.84
Shannons' Diversity		
Season	0.71	0.57
Ants	2.2	0.17
Reptilia		
Richness		
Season	1.4	0.3
Ants	2.1	0.17
Shannons' Diversity		
Season	2	0.19
Ants	2	0.18
Shannons' Evenness		
Season	1.5	0.25
Ants	15	0.002
Mammalia		
Richness		
Season	1.8	0.19
Ants	0.21	0.65

Table 4. Effects of habitat variables on vertebrate abundance values at five forested sites in southern Georgia, U.S.A. based on results of distance-based model. See text for details about each habitat variable.

	F	P
Distance to nearest building	2.5	0.053
Distance to nearest edge	2.5	0.059
Distance to nearest overstory tree	.77	0.54
Distance to nearest road	3.6	0.018
Distance to nearest snag	.86	0.50
Distance to nearest understory tree	.67	0.65
Maximum canopy cover	1.6	0.20
Patch area	1.7	0.14

biodiversity. For example, amphibians have seasonal patterns of breeding (Vignoli, Bologna, and Luiselli 2007; Watling and Donnelly 2002), and it is likely these patterns drove the observations of the genera *Bufo* and *Lithobates*

(Table 1). *Bufo* species breed during the spring and early summer, and *Lithobates* species breed in the late fall and winter (Jensen et al. 2008). All of the amphibian genera we observed are more fossorial during the summer months, especially *Gastrophryne*, which begins breeding in early spring (Jensen et al. 2008). Certain genera in the class Reptilia also showed distinct seasonal patterns in their utilisation of cover boards. *Anolis* was observed much more in the fall and winter, and this also corresponds with their breeding activity (Gorman and Licht 1974; Orrell et al. 2004). *Scincella* was observed more during the fall and winter in our study (Table 1). Although this does not correspond with their breeding activity (Jensen et al. 2008), they have been shown to thermoregulate much more effectively in the fall and winter (Parker 2014). *Eumeces* displays breeding activity in the spring or early summer, and this corresponds with our observations (Trauth 1994; Table 1). *Eumeces laticeps* even aggregates underground for hibernation during cold months (Jensen et al. 2008). Given the proportion of reptiles we observed, it is likely that these seasonal patterns in Reptilia alone drove the seasonal variation in Figure 1. The cotton mouse (*Peromyscus gossypinus*) was observed many times during the fall and winter, but at no point during the spring and summer (Table 1). Although *P. gossypinus* can be active all year, its activity tends to increase during breeding (sometimes in spring, but more often in fall), especially for females in estrus (Cushing and Cawthorn 1996; O'Farrell 1974). It is plausible that the presence of active-foraging snake species (e.g. *Coluber constrictor*, which was observed with much more frequency in the spring/summer: Table 1) may have led to the disappearance of *P. gossypinus* under cover boards in the spring and summer. Clearly, biodiversity studies should continue to collect data across seasons to account for the seasonal activity patterns of the taxa involved.

Our results indicate that vertebrate diversity may have been influenced by the presence of ants under cover boards. The red-imported fire ant (*Solenopsis invicta*) is a dominant invasive species in the southeastern U.S. A. and tends to displace native ants and prey upon small mammals, reptiles, and amphibians (Allen, Demaris, and Lutz 1994; Porter and Savignano 1990; Todd et al. 2007). Although *S. invicta* can discourage the presence of vertebrates under cover boards (Heyer et al. 1994), it is likely that the positive covariation between class diversity and presence of ants found in our study was driven by the large proportion of lizards observed in our study. *Anolis*, *Eumeces*, and *Scincella* composed 58% of our observations throughout the study (Table 1). Although these species may be negatively affected by *S. invicta*, their primary diet is ants (including, *C. floridanus* and *C. pennsylvanicus* which were the other

species of ants we observed) and other insects (Jensen et al. 2008; Martof et al. 1989). Future work could disentangle the positive (food source) and negative (predation risk) effects of ants on refuge use by vertebrates by identifying specific ant species under cover objects or, better, excluding certain species and monitoring potential shifts in vertebrates' use of cover objects (e.g. Stahlschmidt, Walman, and Mills 2018).

Although cover object surveys are a common method to sample biodiversity (e.g. Costall and Death 2010; Grant et al. 1992; Houze and Chandler 2002; MacNeil and Williams 2014), one of their limitations is that animals may use other, more thermally stable refuges (e.g. subterranean burrows) during periods of unfavourable surface temperatures (Houze and Chandler 2002). While cover objects are typically positioned on the ground (e.g. Grant et al. 1992; Hampton 2007), this method has been expanded to include arboreal cover boards (e.g. foam and cardboard strapped around a tree trunk), which can increase observations of both arboreal vertebrates (Nordberg and Schwarzkopf 2015) and invertebrates (Hodge et al. 2007; Lettink and Patrick 2006). The utilisation of cover objects by animals can also be enhanced by designing cover objects to resemble natural refuges, which has been successful in restoring degraded habitats (Bowie et al. 2014) and vulnerable species (Souter, Bull, and Hutchinson 2004). Thus, we recommend the continued use of artificial cover objects in studies of biodiversity because of their numerous advantages: low cost and labour intensity (Kjoss and Litvaitis 2001), properties that encourage utilisation by animals (e.g. protection from predators: Fitch 1992), and less weather-dependent than other methods, such as pitfall traps (Wilson, Mulvey, and Clark 2007).

Our results provide new insight into how variation in forest structure and season alter the abundance and diversity of vertebrates in the southeastern U.S.A. D-road was the only structural variable we found to be a significant indicator of vertebrate diversity, but the distance to edges and buildings also approached significance (i.e. $P = 0.059$ and $P = 0.053$, respectively: Table 4). Two of our other variables (distance to nearest snag and overstory tree) may be more important indicators in landscapes that have been more intensively altered by humans (e.g. agriculture or urban core) (Harvey et al. 2006). Our results also indicate that activity patterns of taxa can influence biodiversity surveys (Dodd 2009; Sung, Karraker, and Hau 2011). Future studies should continue to quantify the role of these ecological drivers of biodiversity (e.g. via manipulations of land management). Because we found location-specific effects (Figure 1; Table 2), our results indicate that vertebrate assemblages may have been driven by urban-rural differences, which have been demonstrated in other

forested ecosystems (Fernández-Juricic 2004; Sutherland 2009; Villaseñor et al. 2014). However, future investigation into more sites (e.g. 10 rural and 10 urban sites) is required to better test for the role of urban-rural differences in our study system. Also, vertebrate abundance may have been influenced by factors not measured in our study, such as thermoregulatory benefits (Engelstoft and Ovaska 2000), environmental moisture (Halliday and Blouin-Demers 2015), and cloud cover (Joppa et al. 2009) – thus, future work could continue to incorporate the effects of a range of factors on patterns of habitat use (e.g. Stahlschmidt and Johnson 2018).

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

George Todd is a biology instructor that teaches general biology and microbiology to traditional as well as dual enrollment students.

Zachary Stahlschmidt is an integrative ecologist that uses snakes and insects to address fundamental biological questions.

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