



Potential influences of forest mesophication on corticolous arthropods as a food base for insectivores in eastern deciduous forests



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ABSTRACT

Decreased disturbance has allowed plant communities in some landscapes to transition from early- and mid-successional communities to later successional communities. In eastern deciduous forests, this process has been termed mesophication because of the transition from a xeric to a more mesic environment. Mesophytic trees tend to produce foliage that is less palatable than xerophytic trees, supporting fewer arthropods that provide an important food source for higher trophic organisms such as insectivorous birds and mammals. An additional characteristic that differs between xerophytic and mesophytic trees is bark texture. Xerophytic tree species tend to produce more deeply furrowed bark that protects trees from overheating. To better understand the potential impact of continued mesophication of eastern deciduous forest on forest dwelling insectivores, we tested the hypothesis xerophytic trees support a greater abundance, biomass, diversity, and richness of arthropods in the Shawnee National Forest of southern Illinois. More specifically, we tested the prediction we would catch a greater number and more diverse community of arthropods on the trunks of white oak (*Quercus alba*) and pignut hickory (*Carya glabra*) trees than on the trunks of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) trees, with tulip poplar (*Liriodendron tulipifera*), a species with an intermediate level of bark roughness and found in both mesic and xeric conditions having an intermediate number of arthropods. Consistent with our prediction, we found the model that included tree species to be most parsimonious when describing variation in arthropod diversity, total arthropod length (as a surrogate for biomass), and arthropod abundance, but not arthropod richness. Differences in arthropod abundance and total length among tree species were driven by the greater total length and abundance of arthropods found on pignut hickory, while the difference in arthropod diversity among tree species was driven by lower Shannon diversity observed on pignut hickory. These results suggest that continued mesophication of eastern deciduous forests may be detrimental to branch and trunk gleaning insectivores, primarily due to the loss of pignut hickory in the forest community. Because both oak and hickory trees support more abundant and diverse foliage dwelling arthropod communities than more mesophytic species, because at least some species of hickory trees support greater total length and abundance of arthropods on their trunk bark, and because species of both genera are most frequently found in more xeric conditions, we recommend forest managers implement management activities that reset succession and maintain a more xerophytic tree community.

1. Introduction

Disturbance patterns have frequently been found to influence floristic community composition (Livingston et al., 2016; Chudomelová et al., 2017; Stambaugh et al., 2017). Anthropically induced reduction in disturbances has impacted composition of various plant communities including forest communities world-wide (Donovan and Brown, 2007; Burkle et al., 2015; Hessburg et al., 2015). Decreased disturbance has

allowed plant communities in some landscapes to transition from early- and mid-successional communities to later successional communities. In the United States, within forested landscapes of the eastern deciduous region, suppressed natural disturbance (e.g. fire) is contributing to a regional change in forest composition via a natural process termed “mesophication” (Nowacki and Abrams, 2008; Hanberry et al., 2012). Historically, upper slopes and ridge tops of eastern deciduous forests were dominated by disturbance dependent xerophytic tree species such

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as oaks (*Quercus* spp.) and hickories (*Carya* spp.), which thrive in the dry, open-canopy conditions maintained by periodic fires from both natural and anthropogenic ignitions (Abrams, 1992; Fralish, 1997). As more urban and agricultural areas were developed throughout the 1900s, however, fire suppression became the main forest management action throughout much of the eastern United States (Nowacki and Abrams, 2008). Reduction in fire frequency across the landscape allowed succession to continue, causing the canopy to close and preventing shade-intolerant oak and hickory seedlings from growing (Nowacki and Abrams, 2008). As this process ensues, understory microclimatic conditions favor shade-tolerant, mesic species (e.g. maples [*Acer* spp.] and American beech [*Fagus grandifolia*]), which in turn outcompete and rapidly replace oaks and hickory. For example, the beech/maple tree community increased by 4,119% in Illinois from 1962 to 1985 (Iverson, 1989). Because the biological impacts of anthropogenic-induced changes to forest composition such as fire suppression are not well understood, appropriate mitigation and remediation for these impacts is difficult to estimate (Fralish and McArdle, 1997; Perring et al., 2015). As such, further insight of how plant species composition influences the abundance, richness, and diversity of higher trophic organisms dependent on resources produced by a given plant composition is needed.

In North America, physical characteristics of xerophytic trees differ from those adapted to mesic conditions in important ways that may impact birds and mammals (Ostfeld et al., 1996; Wolff, 1996; McShea, 2000; Clotfelter et al., 2007). Because of these differences, continued mesophication of eastern deciduous forests has led ecologists to voice concerns over the long-term ability of the forests to support forest-dwelling insectivorous organisms (Askins and Philbrick, 1987; Hagan et al., 1992; Valiela and Maartinetto, 2007). For example, a number of studies investigating arthropod availability among the foliage of trees found arthropods in xerophytic trees to be more prevalent than in more well defended mesophytic tree species (Futuyma and Gould, 1979; Butler and Strazanac, 2000; Summerville et al., 2003a, 2003b; Sierzeza and Eichholz, 2019); potentially influence insectivore population distribution and population dynamics (Holmes and Robinson, 1981; Newell and Rodewald, 2012; Gillen and Hellgren, 2013).

An additional characteristic that differs between xerophytic and mesophytic trees is bark thickness and texture. Xerophytic tree species tend to produce more deeply furrowed bark that protects trees from overheating due to direct sunlight and fire (Nicolai, 1986; Schafer et al., 2015). While the benefits of less well defended foliage to birds are becoming better understood, less research has been conducted on how bark morphology may influence bark gleaning insectivorous organisms. For example, caching and bark gleaning birds forage on the arthropods that use furrows in bark for cover, for foraging, or as travel routes when moving from the ground to tree foliage (Beal, 1911; Williams and Batzli, 1979; Andre, 1985; Nicolai, 1986). Nicolai (1986) found that smooth-barked trees have higher overall surface temperatures, whereas fissured bark provides shaded areas and a variety of microclimates across the bark surface. This variation in microclimate on the bark surface among species has significant impacts on the arthropod community (Nicolai, 1986; Horn and Hanula, 2002). For example, the surface heterogeneity of oak and hickory trees relative to the smoother surface of maple and beech trees is thought to provide increased niche space for arthropods (Jackson, 1979). MacFarlane and Luo (2009) developed a Bark Fissure Index (BFI) to measure the bark surface heterogeneity in tree species in eastern forests. Bark fissure index values assigned to each species were based on the frequency and depth of fissures along a circumference at breast height (about 1.5 m) for a range of sizes. Of the species relevant to this study, the two xerophytic species, white oak (*Quercus alba*, BFI = 28.0) and pignut hickory (*Carya glabra*, BFI = 32.0) had higher BFI values than the two mesophytic species American beech (*Fagus grandifolia*, BFI = 0.9), sugar maple, (*Acer saccharum*, BFI = 13.0), with tulip poplar (*Liriodendron tulipifera*), a species found in both mesophytic and xerophytic conditions, being

intermediate (BFI = 23.6; MacFarlane and Luo, 2009). Bark fissures benefit arthropods directly by producing more suitable living conditions (temperature and moisture gradients and cover), and indirectly by better supporting epiphytes which can provide the basis for the higher trophic community (Andre, 1985; Nicolai, 1986).

In our study area, mesophication of upper slopes and ridge tops is occurring in the Shawnee Hills ecological section of the Shawnee National Forest as evidenced by the increased relative basal area of sugar maple, leading to a patchwork on ridge tops of oak-hickory and beech-maple sites (Fralish et al., 1991; Fralish and McArdle, 2009). Similarly, the relative basal area of many oak and hickory species are decreasing at the same sites and the mesic conditions in these areas are expanding to higher elevation sites due to prevalence of mesic species in the understory (Fralish et al., 1991; Thompson, 2004). To better understand the potential impact of continued mesophication of eastern deciduous forests on forest dwelling insectivores including the 5 species of bark gleaning birds, white-breasted nuthatches (*Sitta carolinensis*), downy woodpeckers (*Picoides pubescens*), red-bellied woodpeckers (*Melanerpes carolinus*), pileated woodpeckers (*Dryocopus pileatus*), and Carolina wrens (*Thryothorus ludovicianus*) that commonly breed in the region, we tested the hypothesis the trunks of xerophytic trees support a greater abundance, biomass, diversity, and richness of arthropods. More specifically, using sticky traps placed on the trunks of trees, we tested the prediction we would catch a greater number and more diverse community of arthropods on the trunk of white oak and pignut hickory trees than on the trunk of sugar maple and American beech trees, with tulip poplar, a species with an intermediate level of bark roughness and found in both mesic and xeric conditions having an intermediate number of arthropods.

2. Materials and methods

2.1. Study area

This study was conducted in the Ozark and Shawnee Hills ecological sections of the 115,740 ha Shawnee National Forest in southwestern Illinois. The Shawnee National Forest was historically a mosaic of tree communities along a moisture gradient represented by 6 ecological land type phases resulting from microclimatic/topographic differences which influenced the intensity and frequency of wildfires (Fralish and McArdle, 2009). The southwest slope, south slope, ridgetop, and north slope ecological land type phases supported xeric conditions that were dominated by *Quercus* spp. and *Carya* spp., while the low slope and terrace ecological land type phases were dominated by mesophytic species such as *Fagus grandifolia* and *Acer* spp. (Fralish and McArdle, 2009). The Shawnee National Forest is primarily 2nd growth timber with past harvest events occurring as either clear cuts, which led to primarily oak/hickory regeneration, or selective harvest of more valuable oak and hickory, creating patches dominated by shade-tolerant species (e.g. beech and maple) that were present in the understory at the time of logging (Fralish and McArdle, 2009). The lack of disturbance and patches of selective harvest has led to discrete patches of mesic tree communities (sugar maple, American beech, and tulip tree) in the upland ridgetop landscape once dominated by oak/hickory. Current forest composition is a mosaic of 37% oak/hickory, 25% mixed-upland hardwoods, 16% beech/maple, and 10% bottomland hardwoods and is dominated by second growth oak/hickory in the uplands and sugar maple, American beech, and tulip tree (*Liriodendron tulipifera*), in sheltered mesic valleys (Thompson, 2004; Fralish and McArdle, 2009). Much of the oak/hickory dominance we see today established during a period of high intensity fire, grazing, and cutting from 1820 to 1930 (Fralish and McArdle, 2009).

2.2. Site selection and sampling design

During 1 – 12 July 2015, we identified 6 sites (3 dominated by oak/

hickory and 3 dominated by beech/maple) with the USFS stand cover map for the Shawnee National Forest (allveg2008.shp) in ArcGIS 10.1.1 (ESRI, Redlands, CA, USA). We used the following criteria for site selection to prevent potential confounding effects with location on the landscape: located within contiguous xeric deciduous forest habitat (i.e., elevation above 120 m), ≥ 12 ha, and not located in riparian areas. Prior to the mesophication of some mesic sites, all sites were xeric and dominated by oak/hickory. Both oak/hickory and beech/maple dominated sites were characterized by mature trees greater than 40 years old, were situated in hilly terrain, and constituted similar northern slopes and aspects. Boundaries of beech/maple dominated sites were distinguished based on the transition of tree communities. Alternatively, because the majority of the landscape that meets the previously described criteria remains a relatively contiguous oak/hickory dominated landscape, boundaries of the more contiguous oak/hickory sites were identified by placing artificial boundaries on Shawnee National Forest cover maps using ArcGIS 10.1.1 (ESRI, Redlands, CA, USA). Differences in tree species composition were due to differences in past harvest techniques, not due to differences in location on the landscape. We uploaded discrete polygon shapefiles of each study site to a handheld Global Positioning System (GPS) for ground-truthing purposes.

To determine tree species dominance within the 6 study sites, vegetation data were collected at 5 random locations distributed as to provide representative coverage of the site. Five points were placed within the core of each site polygon systematic-randomly at a distance of > 75 m from the edge of discrete non-oak forest site and > 125 m from oak-hickory site boundaries. Artificial boundaries of the oak-hickory sites were used because most ridge tops are composed of contiguous forests of oak/hickory. We estimated site basal area (BA) and forest composition at each of the 5 points using a forestry prism (factor: 10; Hovind and Rieck, 1970) for living trees with diameter at breast height (d.b.h.) > 10 cm. We calculated relative basal area (RBA) of (1) oak/hickory species and (2) mesic species (i.e. maple spp., American beech and tulip tree), respectively, by dividing the sum of the BA for each category by the sum of the basal area of all species $\times 100$ for each site (Cade, 1997). All sites were > 12 ha, were > 250 m from major roads, were located at least 125 m away from riparian zones and major water sources, and were dominated by either $> 90\%$ xerophytic (3 sites) or $> 90\%$ mesophytic (3 sites) tree species. In the xeric sites, the dominant species were pignut hickory (*Carya glabra*) and white oak (*Quercus alba*) and in mesic sites, the dominant species were American beech (*Fagus grandifolia*), sugar maple (*Acer sachharum*), with tulip poplar (*Liriodendron tulipifera*) occurring in both communities.

At each vegetation data collection point, three trees were chosen by setting a 10 m radial circle around the point and selecting focal tree species of 15–50 cm d.b.h. within the circle. If more than three appropriate-sized trees were present in the circle, the trees were chosen based on even representation of focal tree species. If fewer than three appropriate trees were present, the circle was expanded and the closest tree fitting the criteria was selected. For each tree chosen, four sticky traps were installed at breast height, one facing in each cardinal direction. The insect traps were non-scented sticky 6.5×13 cm cardboard traps from Catchmaster® that were folded into an open-ended box, excluding the majority of flying insects (Eichholz et al., in press). Under each trap, an area of bark was scraped with a bark scraper to ensure that insects moving through grooves in the bark were funneled into the trap and could not pass underneath. Traps were removed after nine days and each arthropod larger than 3 mm was identified using a guild classification system and its total body length was measured. All arthropods smaller than 3 mm were removed from analysis because their importance as a food resource is likely minimal for most bark-gleaning birds (Beal, 2011). Trapping effort was calculated for each tree by subtracting the length of tree diameter trapped from the diameter at breast height to account for the variation in d.b.h. of trees and the concern that the proportion of each trunk trapped might influence the

quantity of invertebrates captured (Moeed and Meads, 1983).

2.3. Data analysis

Invertebrate data were analyzed using generalized linear mixed models (package lme4 in R version 3.6.0; R Core Team, 2019) with either abundance, richness, total length (surrogate for biomass), or Shannon diversity as dependent variables; forest type, tree species, and trapping effort as independent fixed variables; and because the data from the four traps on each tree were summed, individual tree was included as the lone random variable. We used Akaike's Information Criterion (AIC) for model comparison. Because we used composition of tree species to identify forest type, forest type and tree species are highly correlated in our data, thus, models including both independent variables were not included. However, we compared models with forest type and tree species to determine which model best explained the variation observed in our data.

To compare arthropod communities among tree species and between xeric and mesic tree species, we used non-metric multidimensional scaling (NMDS) in the vegan package (Oksanen et al., 2019) in R studio. NMDS is a common technique for community analysis (Duney et al., 2000) that uses rank orders instead of absolute abundances to compare abundances of multiple different community groups and visualize them in a reduced number of dimensions. First, we used NMDS to create a dissimilarity matrix among the different arthropod groups using the Bray-Curtis dissimilarity coefficient. We chose to represent the data in 2 dimensions. To check that 2 dimensions sufficiently retained the dissimilarities of the original data, we created a stress plot which compares the distances between each group and their original dissimilarities. We then plotted the NMDS data using the R package ggplot2 (Wickham, 2016). We categorized the different arthropod groups by forest type (mesic vs. xeric) and then by the type of tree on which they were sampled (poplar, oak, maple, etc.).

3. Results

We collected arthropod data from the trunks of 54 individual trees (12 pignut hickories, 15 white oaks, 8 American beeches, 12 sugar maples, and 7 tulip poplars) among the 6 sites. We identified individuals from 22 of the 27 guilds known to occur in the area based on Sierzeza and Eichholz (2019), with each tree species supporting at least 19 of the 22 guilds and each individual tree supporting at least 7 of the 22 total guilds identified. Based on the AIC values, although none of the models explained a substantial portion of the variation, the models that included tree species were the most parsimonious in explaining marginal variation in total arthropod length ($R^2 = 0.02$), abundance ($R^2 = 0.02$), and diversity ($R^2 = 0.06$), while none of our independent variables explained substantial variation in richness (Table 1). In addition, with the possible exception of richness, proportion of the tree trapped (effort) appears to have no substantial influence on any of the dependent variables (Table 1).

We found no strong evidence corticolous arthropod richness was influenced by tree species or habitat type. Alternatively, for Shannon diversity, the model that included mean arthropod Shannon diversity was lowest on pignut hickory trunks and highest on tulip poplar, a species found in both xeric and mesic conditions (Fig. 1). This contrasted with both abundance and total length which was lowest in tulip poplar and highest in pignut hickory (Fig. 1).

Based on the NMDS analysis, there was no clear difference in arthropod community structure between the mesic and xeric tree species (Fig. 2). When comparing the differences of the arthropod community among tree species, however, tulip poplars appear to support a different arthropod community than either American Beech or pignut hickory (Fig. 3).

Results of a 2 dimensional non-metric multidimensional scaling (NMDS) analysis using the Bray-Curtis dissimilarity coefficient to create

Table 1
Statistical model results.

Dependent variable	Model	K ^a	AIC	ΔAIC
Richness	Null	2	210.56	0
	Tree species	7	211.69	1.13
	Effort	3	211.93	1.37
	Forest type	4	212.54	1.98
Total body length	Tree species	7	719.69	0
	Forest type	4	724.45	4.76
	Null	2	727.00	7.31
	Effort	3	728.96	9.27
Abundance	Tree species	7	495.55	0
	Forest type	4	499.83	4.27
	Null	2	501.04	5.48
	Effort	3	503.04	7.48
Diversity	Tree species	7	28.78	0
	Forest type	4	36.99	8.21
	Null	2	37.31	8.52
	Effort	3	38.72	9.93

Results of mixed model Analysis of Covariance with either arthropod richness, Shannon diversity, abundance, or total length (as a surrogate for biomass) as the dependent variable, sample tree as a random categorical variable, tree species (pignut hickory, white oak, American beech, sugar maple, and tulip poplar) and forest type (xeric or mesic) as fixed categorical variables, and capture effort as the lone continuous fixed variable. The null model includes only the intercept and random variable. Arthropods were captured with sticky traps placed on the trunks of trees July 2015.

^a K equals the number of model parameters.

a dissimilarity matrix among the different arthropod groups. We created a stress plot to compare the distances between each group and their original dissimilarities to check that 2 dimensions sufficiently retained the dissimilarities of the original data. We then plotted the NMDS data by forest type (mesic vs. xeric).

Results of a 2 dimensional non-metric multidimensional scaling (NMDS) analysis using the Bray-Curtis dissimilarity coefficient to create a dissimilarity matrix among the different arthropod groups. We created a stress plot to compare the distances between each group and their original dissimilarities to check that 2 dimensions sufficiently retained the dissimilarities of the original data. We then plotted the NMDS data by tree species on which they were sampled (American beech, pignut hickory, sugar maple, white oak, and tulip-poplar).

4. Discussion

Disturbance-dependent climax community tree species have evolved specific characteristics that enable them to thrive in direct sunlight and withstand frequent disturbances such as periodic fires (White, 1983; Nicolai, 1986, 1991). These species tend to be less tolerant of shade, grow more quickly, and produce foliage with fewer chemical defenses; thus, are more susceptible to herbivory, supporting a greater abundance and diversity of arthropods (Futuyama and Gould, 1979; Stamp, 2003; Summerville et al., 2003a, 2003b). Although a number of authors have addressed how the process of mesophication may be detrimental to foliage-dwelling insectivorous forest birds and mammals due to a decrease in biomass of arthropods and hard mast, little attention has been given to how the process influences insectivorous birds and mammals that use resources associated with the bark of tree branches and boles (Holmes and Robinson, 1981; Martel and Mauffette, 1997; Butler and Strazanac, 2000; Rodewald and Abrams, 2002; Summerville et al., 2008; Gillen and Hellgren, 2013). Understanding how forest management actions may impact the entire suite of forest dependent organisms will be important for making future management decisions.

Greater abundance of corticolous arthropods is often used to explain the more frequent use of oak-hickory sites by bark-gleaning birds (Kilham, 1970; Travis, 1977; Mariani and Manual, 1990; Rollfinke and

Yahner, 1991). Additionally, multiple authors have found greater abundance of resident corticolous arthropods on tree boles with more fissured bark, the type of bark found on most species of oak and hickory trees (Nicolai, 1986, 1989; Stubbs, 1989; Miller et al., 2007). Because of the greater bird use on trees with more deeply furrowed bark and previously described benefits of furrowed bark to arthropods, we expected to find greater abundance, biomass, richness, and diversity of corticolous arthropods on the bark of pignut hickory and white oak and a positive association between abundance and richness of arthropods, as has been found in other studies (Jackson, 1970; Wilson, 1970; Conner, 1980; Rollfinke and Yahner, 1991; Rodewald and Abrams, 2002).

We found evidence that during the first 2 weeks of July, a time post-fledged young from early-season nests are foraging on their own and adults are feeding pre-fledged young from late-season nests, pignut hickory, a mid-successional species commonly found in eastern deciduous forests but decreasing in abundance due to reduced disturbance, supports a larger abundance and biomass of arthropods than the mesophytic trees that are replacing them. We have no ability to estimate how this result may vary annually. This result may be especially relevant to birds in that about 70% of the arthropods we collected were in the orders Hymenoptera (62%) and Orthoptera (8%), orders previously described to be important in the diet of bark gleaning birds (Beal, 1911; Jackson, 1979; Williams and Batzli, 1979). Somewhat to our surprise, however, tree species explained only a small portion of the observed variation and arthropod abundance and biomass was substantially lower in tulip poplar, a tree with intermediate bark roughness. Furthermore, the similar values of arthropod metrics among tree species with very different BFI values (white oak, beech, and sugar maple) and the lower values we observed on tulip-poplar trees were inconsistent with predictions. This suggests something other than bark texture is driving variation in the corticolous arthropod communities in our study (Franzreb, 1985; Petit et al., 1989; Nicolai, 1986; Mariani and Manual, 1990; Woodrey, 1991; Prinzing, 2001).

Most previous studies that have found a strong association between arthropod communities and bark texture focused on resident arthropods that spend their entire life cycle on tree boles (Nicolai, 1986, 1989; Stubbs, 1989; Miller et al., 2007). The positive relationship between bark texture and arthropod communities, however, is not ubiquitous (Majer et al., 2003). In fact, studies that include more transient species, crawling arthropods that use tree boles as travel routes from the ground to higher foliage and flying arthropods that use tree boles for cover or as resting sites, often find only a weak or no relationship between bark texture and arthropod community metrics (Mariani and Manuwal, 1990; Hanula and Franzreb, 1998; Hanula et al., 2000; Proctor et al., 2002; Majer et al., 2003). We captured arthropods over a 9-day period with sticky traps that capture both crawling and flying arthropods, thus, a large component of our arthropods were transient. This may explain why, although bark texture appears to have had some influence, most of the variation in corticolous arthropod community was unexplained and appears to be driven by other factors.

A number of other factors have been used to explain variation of the more transient corticolous arthropod community including management activities (Miller et al., 2007; Duguay et al., 2000) epiphyte abundance (Stubbs, 1989; Miller et al., 2007), landscape (Le Roux et al., 2018) composition of forest understory (Jackson, 1979; Hanula and Franzreb, 1998; Hanula et al., 2000; Duguay et al., 2000; Collins et al., 2002; Halaj et al., 2009), presence of invasive species (Ulyshen et al., 2010), and host tree species (Yasuda and Koike, 2009). In our study, the white oak arthropod community metrics we measured were more similar to the American beech and sugar maple than the pignut hickory, even though the white oak and pignut hickory trees were found in the same plant community and in very close proximity (typically < 10 m apart), while the white oak trees were found in a different plant community than the beech and sugar maple. Additionally, the abundance and biomass of the arthropod community captured on the tulip poplar

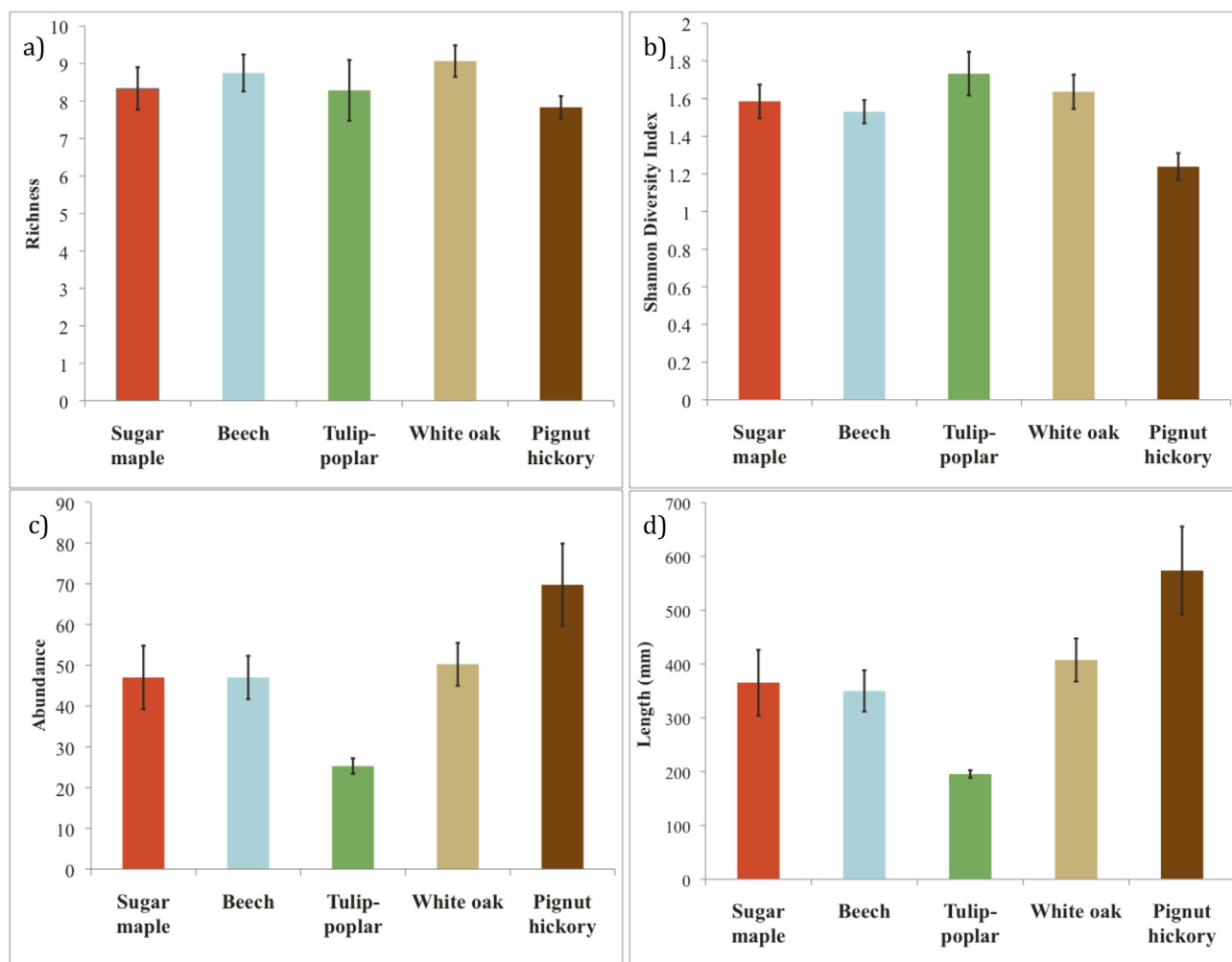


Fig. 1. Tree species-specific variation of corticolous arthropods. Least square means (\pm SE) derived from the most parsimonious model of arthropod richness (a), Shannon diversity (b), abundance (c), and total length as a surrogate for biomass (d) for each tree species from sticky traps placed on trees in July 2015 on the Shawnee National Forest, Illinois, USA.

appears to be different from all other species, even though the tulip poplars were within the same plant community and within a few meters of the individual sugar maple and American beech trees. These results suggest the observed variation was not due to management activity,

landscape characteristics, composition of the forest understory, or presence of invasive species. The most likely factor to explain the variation in arthropod metrics we observed is species specific variation of an intrinsic characteristic of the tree other than bark texture (Yasuda

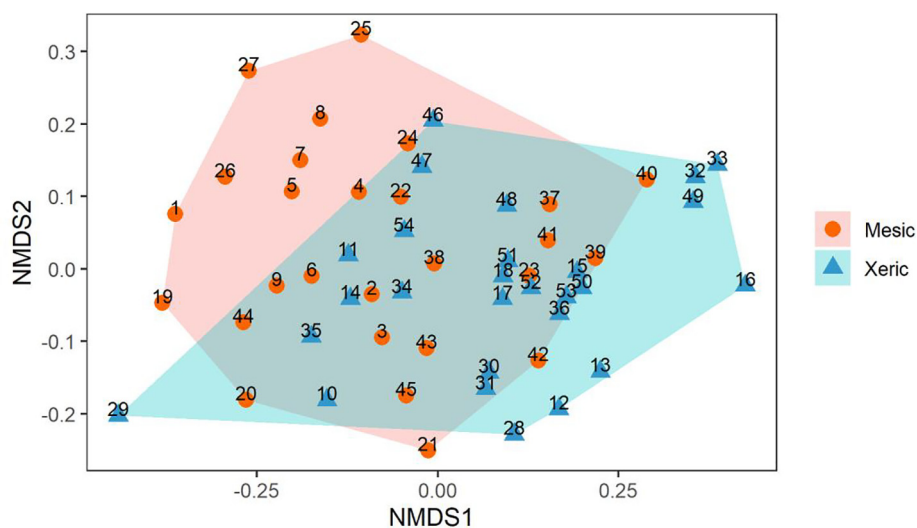


Fig. 2. Results of NMDS comparing arthropod communities between xeric and mesic trees.

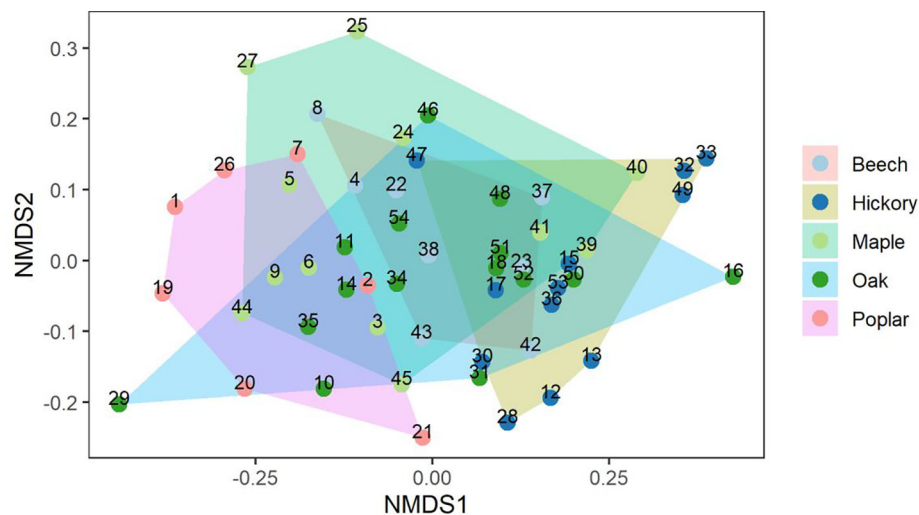


Fig. 3. Results of NMDS comparing arthropod communities among the 5 species of trees.

and Koike, 2009). As with these results, in a companion study we found foliage-dwelling arthropods to be most abundant and diverse in the foliage of pignut hickory (Sierzega and Eichholz, 2019). This suggests the palatability of the tree foliage may influence both the foliage-dwelling and corticolous arthropod communities. More palatable foliage may attract to the upper foliage more arthropods that spend part of their diurnal cycle on the ground or may provide more palatable leaf litter that supports a greater abundance of generalist arthropods that use both the ground and tree bole (Moeed and Meads, 1983). In the same study, however, we found the foliage of tulip poplar to support an abundance and biomass of arthropods considerably higher than that of oak, maple, or beech trees, while corticolous arthropod abundance and biomass of tulip poplar was considerably lower than those species in this study, contradicting this explanation (Sierzega and Eichholz, 2019). Thus, the relationship between foliage and corticolous arthropod communities is at best inconsistent. Finally, we did not quantify corticolous epiphytes in our study, thus have no ability to infer how they may have influenced arthropod communities.

Some previous studies have found a positive association between corticolous arthropod abundance and richness or diversity (Nicolai, 1986). In our study, pignut hickory supported the greatest abundance and biomass of corticolous arthropods among the five trees species we studied, however, we found no evidence arthropod richness varied among trees species while pignut hickory supported the lowest level of Shannon diversity. The primary objective of our study was to investigate how changes in the tree community caused by mesophication may indirectly influence higher trophic insectivorous organisms through its impact on corticolous arthropod communities. Because most insectivorous birds and mammals are generalists that feed on a variety of arthropods, we limited our arthropod identification to functional guilds and orders. It's possible, a more detailed taxonomic evaluation of the arthropods in our study would provide different results, but the effort needed for such analysis was beyond the scope of this study. In pignut hickory, low diversity scores were likely due to a high abundance of Hymenoptera, primarily ants which composed approximately 62% of the abundance arthropods on pignut hickory. This unevenness in the individuals among taxonomic units caused the arthropods found on pignut hickory to have a lower diversity score.

5. Management recommendations

In eastern deciduous forests, upper slopes and ridge tops burn hotter and more frequently than low slope and terrace ecological land types, thus support a more xerophytic tree community (Wright and Bailey,

1982). This study supports mounting evidence that some species of fire dependent mid-successional trees that compose this more xerophytic community support a higher biomass of arthropods that make up all or part of the diet of insectivorous forest-dwelling birds and mammals in both their bark and foliage. An anthropically induced reduction in disturbances has been observed in forest communities worldwide (Vitousek et al., 1997; Haberl et al., 2007; Morris, 2010; Baraloto et al., 2012). This modification to disturbance regimes is troubling from the perspective of forest bird conservation in that results of studies on foliage dwelling arthropods suggests forest mesophication will impact resources availability for insectivorous foliage dwelling birds, a group of birds already in decline (Rodewald and Abrams, 2002; Newell and Rodewald, 2012).

While only one species of xerophytic tree (pignut hickory) in our study supported greater corticolous arthropod abundance and biomass than the more mesophytic species, because the corticolous arthropod abundance and biomass was similar between white oak, sugar maple, and beech trees, management actions that support the growth of white oak for their benefit to foliage dwelling insectivores would not be detrimental to bark dwelling insectivores. Additionally, even if more fissured bark does not consistently support a greater abundance and biomass of corticolous arthropods across all tree species, previous studies indicate bark dwelling insectivores prefer the more fissured bark for other reasons such as decreased energy expenditure in that more fissured bark requires less movement by insectivores to search a greater surface area of bark (Franzreb, 1985; Mariani and Manuwal, 1990). Additionally, bark dwelling birds may prefer more fissured bark because of morphological adaptations (Conner, 1980, 1981; Lundquist and Manuwal, 1990), a greater number of locations for caching captured food (Petit et al., 1989; Woodrey, 1991), climatic conditions (Grubb, 1977, 1978, 1979; Lundquist and Manuwal, 1990), and competition within and among species (Jackson, 1970; Willson, 1970, 1971; Williams and Batzli, 1979; Franzreb, 1985). Thus, for the benefit of bark dwelling insectivores, we recommend management actions that reduce the mesophication process and promote xerophytic tree species.

At the time of our study, the discussion involving the potential impacts of mesophication on insectivorous wildlife has emphasized the loss of oak trees that occurs during the process. While oak trees provide substantial mast that is an important resource for forest wildlife, these results as well as the results of our companion study suggest the impact of mesophication on hickory trees should receive greater consideration (Sierzega and Eichholz, 2019). Additionally, although the white oaks in this study were not observed to support greater arthropod resources than the more mesophytic trees, most xerophytic oak trees thrive under

the same ecological conditions and are often found in association with xerophytic hickories, thus management actions that benefit oaks should also benefit the hickories that appear to be even more beneficial to forest dwelling insectivores.

As evidenced by this study and others, continuing mesophication could reduce the abundance and diversity of bark-gleaning species. Woodpeckers and nuthatches provide important ecological functions, such as cavity creation, control of insect populations, reduction in numbers of harmful insects and consequent improvement in tree health (Sekercioglu, 2006). Additionally, the transition in plant communities could impact small and medium sized mammals which feed on the mast, and in some cases arthropods, and play a crucial role in the overall forest food web (Whitaker, 1963; Semel and Anderson, 1988; Ostfeld et al., 1996; Aldrich et al., 2005). Although the ideal solution would be to restore the historical disturbance regime through controlled burns, social considerations often prevent this practice from occurring. Alternative methods of creating disturbances in these mid-successional disturbance dependent landscapes such as tree harvest that promotes the growth of xerophytic tree species needs to be further explored if the current level of habitat for forest dwelling insectivores is to be maintained. Furthermore, results of our study indicate that while the species of tree with the greatest BFI supported the greatest biomass of bark dwelling arthropods, there was no clear relationship between BFI and arthropod community. Thus, additional studies on the factors that influence arthropod biomass in tree bark and the potential impact of a decline in bark and foliage dwelling arthropods on insectivorous forest dwelling organisms should be conducted.

CRediT authorship contribution statement

Elise Zarri: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. **Michael W. Eichholz:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing, Supervision, Funding acquisition. **Kevin P. Sierzega:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - review & editing.

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