CONSERVATION ECOLOGY – ORIGINAL RESEARCH

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Linking conservation implications of modified disturbance regimes, plant communities, plant associations, and arthropod communities

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Abstract

Modifications to disturbance regimes have landscape-level effects on plant communities and have the potential to influence organisms at multiple trophic levels. We examined differences in the arthropod community across a gradient of oak/hickory dominance, a plant community maintained by disturbance such as periodic fires and extensive land clearing. In southern Illinois, we used patches of forest that varied in tree dominance ranging from 94 to 0% oak/hickory composition dependent on prior land usage that occurred > 50 years ago at minimum, to test two predictions: (1) oak (*Quercus*) and hickory (*Carya*) species contain more arthropod biomass and diversity than mesic tree species [e.g., American beech (*Fagus grandifolia*) and maples (*Acer* spp.)] and (2) due to plant associations, arthropod communities are more diverse and abundant on host trees within oak/hickory stands than non-oak/hickory stands. Our results were consistent with the prediction that arthropod biomass, guild Shannon diversity, and guild richness are higher on oaks, hickories and tulip tree (*Liriodendron tulipifera*) than beech and maples. We also found support for the prediction that due to plant associations, % non-oak/hickory stand composition negatively influenced arthropod guild Shannon diversity and guild richness on host trees, including maples and beech. These results are the first to demonstrate that modified disturbance regimes can influence multiple trophic levels both directly due to species-specific variation in susceptibility of plants to herbivory and indirectly through effects of plant associations. This result is concerning as modified disturbance regimes are influencing large-scale plant community composition among biomes worldwide.

Keywords Disturbance · Diversity · Trophic interactions · Plant association · Succession

Introduction

The impact of human activities has dramatically altered terrestrial landscapes, with approximately 20% of the earth's surface now dominated by humans and 39–50% substantially altered (Vitousek et al. 1997; Haberl et al. 2007; Morris 2010; Baraloto et al. 2012). These anthropogenic influences have decreased biodiversity to the extent that loss

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of diversity itself is now acting as a mechanism of global change; that is, loss of diversity within one guild occurs directly from anthropogenic influences impacting diversity of other guilds, often through trophic interactions (Hunter and Price 1992; Forkner and Hunter 2000; Sala et al. 2000). Thus, a better understanding of how landscape changes influence the interactions between communities of plants and animals at multiple trophic levels is of interest from both a basic and applied ecological perspective (Fischer et al. 2010; Perring et al. 2015). A limited number of studies have demonstrated variation in abundance, diversity, and richness of higher trophic organisms associated with differing plant communities within and among biomes (Hooper et al. 2005; Scherber et al. 2010). A mechanism influencing differences among plant communities within biomes is variation in resource availability, which in turn can influence the community composition of higher trophic organisms (Mittlebach et al. 2001; Hurlbert and Haskell 2003; Bailey et al. 2004; Gillen and Hellgren 2012; Whitfeld et al. 2014).

Floristics and composition of plant species have been altered via anthropogenic-induced decreases in disturbance across a variety of forest biomes worldwide (Livingston et al. 2016; Chudomelová et al. 2017; Stambaugh et al. 2017). Over recent decades within forested landscapes of the eastern deciduous region, suppressed natural disturbance (e.g., fire) contributed to a regional change in forest composition via a natural process termed "mesophication" (Nowacki and Abrams 2008; Hanberry et al. 2012). 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 out-compete and rapidly replace oaks (*Quercus* spp.). 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 are difficult to estimate (Fralish and McArdle 2009; 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.

To examine the effects of anthropogenic-induced changes on plant compositions and the associated biological implications, we compared arthropod communities found in the mid-layer canopy between tree communities. Arthropods contribute a large proportion of faunal diversity in forests and play a crucial role in ecosystem processes by directly suppressing primary productivity via herbivory (Schowalter et al. 1986; Summerville and Crist 2002). In turn, plant defenses against herbivory strongly influence lower trophic levels via bottom-up effects (Hunter and Price 1992; Scherber et al. 2010). The level of plant defenses varies among and within species and includes morphological characteristics (e.g., spikes and barbs) and chemical toxins, often specific to the host tree and herbivore, which render vegetation unattainable and less palatable. Chemical defenses regulate abundance and assemblage of herbivores (Ehrlich and Raven 1964; Feeny 1968), which in turn influence food availability for secondary consumers.

In addition to host tree specificity, the presence and specificity of neighboring host trees influence both biomass and richness of arthropod herbivores (Barbosa et al. 2009). The presence or absence and species composition of neighboring plants have been found to both positively (associational susceptibility) and negatively (associational resistance) influence herbivory and herbivore abundance on host plants (Root 1973; Brown and Ewel 1987; Barbosa et al. 2009). Associational susceptibility is proposed to occur via resources concentrating herbivores in patches with greater availability of palatable plants or via herbivores spilling over to the host plant from the more palatable neighboring plants, increasing herbivory to the less preferred host (Brown and Ewel 1987; White and Whitham 2000; Jactel and Brockerhoff 2007). Alternatively,

associational resistance is thought to primarily occur via either the "enemies hypothesis" or reduced "host plant apparency" (Root 1973; Feeny 1976; Castagneyrol et al. 2013). The enemies hypothesis postulates that because a more diverse plant community supports a greater abundance of enemies (parasites and predators), the abundance of herbivores on host plants within a more diverse plant community is lower (Root 1973). Alternatively, the plant apparency hypothesis posits associational resistance occurs because apparency of host plants is lower when host plants are surrounded by less palatable species (Feeny 1976, Castagneyrol et al. 2013).

While previous studies of plant associations have emphasized the impact of herbivory on host species, our interests focus on the impact of plant associations on the prevalence of prey for higher trophic predators such as forest insectivores (e.g., birds). Plant associations may affect higher trophic organisms by influencing the biomass or diversity of herbivores on host plants and, thus, the availability of arthropod herbivores as a food source for higher trophic predators (Hunter and Price 1992; Forkner and Hunter 2000; Scherber et al. 2010). For example, Lepidoptera contribute a large proportion to insectivorous songbird diets (Holmes and Robinson 1981). Therefore, the process of mesophication may not only decrease food resources for higher trophic organisms by directly reducing the number of more palatable trees, but also by reducing the abundance and diversity of arthropods found on oak or hickory trees remaining in the more mesic plant community.

To address these questions, we tested two primary predictions within forest communities representing a gradient of oak and hickory (*Carya* spp.) dominance in the Shawnee National Forest (SNF) of southern Illinois. First, because oak and hickory species are mid-successional and exhibit moderate-to-no shade tolerance, we predicted that they are more palatable and, thus, contain more arthropod biomass, guild Shannon diversity, and guild richness than late-successional species (e.g., beech and maple). Second, we tested for evidence that surrounding forest composition influences arthropod biomass, guild Shannon diversity, and guild richness on host trees. We predicted via either the plant apparency or enemies hypotheses that arthropod biomass, guild Shannon diversity, and guild richness on host plants would be higher when host plants are in stands dominated by presumably more palatable oak and hickory species than in stands dominated by less palatable beech and maples.

Materials and methods

Study area and site selection

We conducted our study in the forested, un-glaciated landscape of southern Illinois throughout the SNF. The

286,000ac SNF is located in the Central Hardwoods region within the Ozarks and Shawnee Hills natural divisions (Schwegman 1975). 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 (Fralish and McArdle 2009; Thompson 2004). 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). Following the designation of the SNF in the 1930s, harvest events, occurring as either clear cuts or selective harvest of more valuable oak, created patches dominated by rapid-growing tulip tree and shade-tolerant species (e.g., beech and maple) that were present in the understory at the time of logging. The landscape underwent cessation of fire over recent decades; as such, current forest composition contains more mesophytic species than historically (Fralish and McArdle 2009).

We selected 22 study sites along an oak/hickory dominance gradient by identifying either oak/hickory or beech/maple-dominated sites with the USFS stand cover map for the SNF (allveg2008.shp) in ArcGIS 10.1.1 (ESRI, Redlands, CA, USA). We used the following criteria for site selection to prevent potential confounding effects: located within contiguous upland-deciduous forest habitat (i.e., elevation above 120 m), $\geq$ 12 ha, and not located in riparian areas. Both oak/hickory and beech/maple sites contained mature trees > 50 years old and were situated in hilly terrain, thus comprising similar slopes and aspects. Boundaries of beech/maple sites were distinguished based on the transition of tree communities while boundaries of oak/hickory sites were identified artificially using SNF cover maps and ArcGIS 10.1.1 (ESRI, Redlands, CA, USA). As the SNF is primarily second growth timber, differences in tree species composition among our sites were representative of past land usage (e.g., clear cuts or selective harvest), not due to differences in location on the landscape; our sites were large forest blocks within un-glaciated terrain. Our study sites have not experienced landscape-level disturbance (i.e., logging) for > 50 years. We uploaded discrete polygon shapefiles of each study site to a handheld Global Positioning System (GPS) for ground-truthing purposes.

Sampling procedures

Vegetation data were collected at five locations in each of the 22 study sites. These 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/hickory sites and > 125 m from artificial oak/hickory site boundaries to provide representative coverage of the site. We estimated

stand basal area (BA) and forest composition at each of the five 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 × 100 for each site (Cade 1997). We used these metrics to classify sites along a gradient of oak/hickory dominance and to identify the landscape in which individual trees were located to test the hypothesis that tree species composition of the surrounding landscape can influence arthropod communities on individual host trees.

We sampled three trees at each of the five vegetation points from each of the 22 previously described sites from 0600 to 1400 h during 23 May to 25 June 2014. We located trees by searching outward to a 30 m radius around each vegetation point until a mature tree > 20 cm d.b.h. with branches low enough to sample was found. In general, the three mature trees closest to the center point that represented three of the five genera (*Acer, Carya, Fagus, Liriodendron,* and *Quercus*) of interest were sampled (Table 1). This procedure, however, led to a sample composition similar to the majority species composition for each site type; i.e., primarily oaks and hickories in oak/hickory sites and beech, maple, or tulip tree in non-oak/hickory sites. Thus, to ensure we had an adequate sample size to test the influence of surrounding forest composition on arthropod communities of host trees, when an individual tree that differed from the majority species composition was located within the 30 m search radius (e.g., beech in an oak/hickory site), we selected it instead of the third closest mature tree representative of the majority species composition. We occasionally sampled smaller d.b.h. trees that differed from the majority species composition when they were the only size class available at our sample locations. Therefore, to control for potential bias associated with tree maturity (Futuyma and Gould 1979; Summersville and Crist 2002), we recorded sample tree d.b.h. and included it as a random continuous variable in all analyses.

Once the tree was located, we collected two arthropod samples in the mid-layer canopy using the branch-bagging technique (Crossly et al. 1976; Johnson 2000). We brought an open bag (13-gallon garbage bag as a sample collection unit) attached to the end of a telescoping pole around a desired branch and then rapidly sealed it to prevent arthropods from escaping (Crossly et al. 1976). We cut the branch proximate to the bag using an 8 m telescoping pruner. Branch bagging is an effective way to sample sedentary arthropods on leaf and branch surfaces and is capable of collecting arthropods from all orders; however, aerial arthropods are underrepresented (Johnson 2000). Because distribution of forest arthropods is heterogeneous in location and

Table 1 Branch-clipping sample descriptions and statistics for Lepidoptera presence in the Shawnee National Forest, USA 2014

Tree genus	Tree species	Shade tolerance level	n	Avg. guild richness	Avg. guild diversity	Avg. biomass/m	Avg. Lep biomass/m	Proportion samples with lepidoptera	# Lep per species
Acer	*rubrum*	Tolerant	2	7.5	1.28	0.01546	0.00122	0.50	1
Acer	*saccharum*	Tolerant	138	3.5	0.85	0.00282	0.00023	0.13	16
Carya	*cordiformes*	Intolerant	10	4.5	0.98	0.00907	0.00212	0.30	3
Carya	*glabra*	Intermediate	79	4.2	1.06	0.01190	0.00188	0.18	9
Carya	*ovata*	Intermediate	37	5.2	1.14	0.02865	0.00097	0.19	2
Carya	*tomentosa*	Intolerant	15	6.1	1.29	0.03058	0.01364	0.27	3
Fagus	*grandifolia*	Very Tolerant	67	3.3	0.81	0.00216	0.00007	0.07	5
Liriodendron	*tulipifera*	Intolerant	70	4.3	1.12	0.01114	0.00147	0.36	20
Quercus	*alba*	Intermediate	117	5.1	1.20	0.00531	0.00053	0.36	27
Quercus	*stellata*	Intolerant	12	4.8	1.00	0.01667	0.00030	0.25	3
Quercus	*muehlenbergii*	Intolerant	23	4.9	1.20	0.00383	0.00015	0.35	2
Quercus	*macrocarpa*	Intermediate	4	6.3	1.11	0.01366	0.00581	0.50	1
Quercus	*rubra*	Intermediate	42	4.2	1.04	0.00720	0.00091	0.17	4
Quercus	*marilandica*	Intolerant	12	3.7	0.96	0.00436	0.00019	0.17	13
Quercus	*imbricaria*	Tolerant	3	2	0.28	0.00322	0.00000	0.00	0
	Sum		631						

m meter of branch

density (Summerville et al. 2003a, b), we sampled both low and high branches that were close and far from the trunk; however, tree structure often dictated sample locations. We alternated sample location in relation to trunk for respective species. Each sample consisted of 30–150 leaves (individual leaflets on compound hickory leaves constituted one leaf).

We froze branch-clipping samples and processed them in the laboratory. We rinsed samples with water to dislodge all arthropods for identification. We grouped arthropods according to a simplified guild classification by diagnostic morphological characteristics (Table 2; Futuyma and Gould 1979). We noted differences between larvae and adults. For each sample, we dried arthropods from each guild, respectively, for 48 h at 45 C to receive dry mass. We calculated total twig length (mm) of each sample by measuring all sections of twig to the bud, beginning at the first branching location.

Data analysis

We predicted that (1) oak and hickory species contain more arthropod biomass, guild Shannon diversity, and guild richness than late-successional species (e.g., beech and maple). To test this, we estimated arthropod biomass (g/m) as biomass divided by total twig length (mm) × 1000. We used generalized linear mixed models with total arthropod biomass (g/m), Lepidopteron biomass (g/m), guild Shannon diversity (H'), or guild richness (total guild richness per sample) as dependent variables; tree genus as a fixed categorical variable ($N = 5$), distance from the trunk (distance) and sample height (height) as fixed continuous variables, sample tree d.b.h. and Julian date as random continuous variables, and unique sample tree nested within unique sample point (1 | point/tree) as a random term with a random intercept to account for variability that may exist within tree species and among sample locations (Zuur et al. 2009). All models were fit in package *lme4* (Bates et al. 2015) using the statistical software R (R Core Team 2014). We considered fixed independent variables to be significant at the 0.05 alpha level and marginally significant at the 0.10 alpha level. We standardized explanatory variables to have a mean of zero to facilitate model convergence prior to analyses. We examined parameter estimates of fixed effects from our top models using restricted maximum likelihood (Zuur et al. 2009).

We predicted that (2) arthropod communities on host trees within oak/hickory sites would have higher biomass and be more diverse (guild Shannon diversity and guild richness) than those within non-oak/hickory sites. To test this prediction, we first tested for a relationship between % oak/hickory composition of the surrounding landscape and the previously identified dependent variables including an interaction between tree genus and % oak/hickory composition. For dependent variables in which the most parsimonious model included the interaction, we tested for a relationship between % oak/hickory composition and the dependent variable for each tree genus separately.

Table 2 Number (#) and percent (%) of branch-clipping samples that contained the identified Arthropod guild from 631 branch-clipping samples in the Shawnee National Forest, USA 2014

Guild	Taxa	Classification specifics	# samples containing guild	% samples containing guild
Prim. wingless hexapods	Order *Apterygota*		86	14
Dragonflies and allies	Order *Odonata*		12	2
Orthopterans	Order *Orthoptera*		91	14
True Bugs 1	Order *Hemiptera*	Stink, assassin, lace, bark bugs	173	27
True Bugs 2	Order *Hemiptera*	Cicadas, leafhoppers, aphids	401	64
True Bugs 3	Order *Hemiptera*	Barklice, booklice, thrips	157	25
Beetles 1	Order *Coleoptera*	Carabid and tiger beetles	2	0
Beetles 2	Order *Coleoptera*	Scarabs and allies	8	1
Beetles 3	Order *Coleoptera*	Fireflies, click beetles, and allies	125	20
Beetles 4	Order *Coleoptera*	Lady, leaf beetles, and allies	64	10
Beetles 5	Order *Coleoptera*	Weevils and allies	69	11
Beetles 6	Order *Coleoptera*	Misc. beetles	99	16
Lepidopterons	Order *Lepidoptera*		149	24
Flies 1	Order *Diptera*	Midges, crane flies, mosquitoes, and allies	134	21
Flies 2	Order *Diptera*	Horse, house, deer, bot, etc. flies	76	12
Hymenopterans 1	Order *Hymenoptera*	Parasitic and gall wasps	40	6
Hymenopterans 2	Order *Hymenoptera*	Bees, ants, wasps, and allies	234	37
Hymenopterans 3	Order *Hymenoptera*	Misc.	0	0
Misc. Holometabola	Order *Nueroptera,* etc.	Dobsonflies, lacewings, caddisflies	130	21
Parasitic Insects	Order *Siphonaptera,* etc.	Fleas, scorpionflies, lice, etc.	7	1
Spiders 1	Order *Araneae*	Mites	90	14
Spiders 2	Order *Araneae*	Spiders	347	55
Harvestmen	Order *Opiliones*		46	7
Millipedes	Class *Diplopoda*		1	0
Centipedes	Class *Chilopoda*		1	0

Results

Site differences

Our 22 study sites ranged from 0 to 94% oak/hickory RBA, 2–48% beech/maple RBA, and 0–60% tulip tree RBA. When combining beech, maples and tulip tree RBA to estimate % non-oak/hickory, our sites ranged from 5 to 92% dominance. Stand basal area ranged from 19 to 29 m^2 ha^{-1}. Site elevation ranged from 139 to 238 m above sea level and mean slope ranged from 10.8 to 47.3%.

Arthropod differences

We analyzed 626 branch-clipping samples from 15 tree species representing five genera across a gradient of oak/hickory dominance (Table 1). We identified arthropods to 25 distinct guilds by diagnostic morphological characteristics (Table 2). Orders *Coleoptera* (presence 0–20% of samples across guilds)*, Diptera* (presence 12–22% of samples across guilds)*, Hemiptera* (presence 25–64% of samples across guilds)*, Hymenoptera* (presence 6–37% of samples across guilds)*, Lepidoptera* (presence 24%), and *Araneae* (presence 14–55% of samples across guilds) were most abundant among samples (Table 2).

All results were consistent with our first prediction. Total arthropod biomass varied by tree genus ($P < 0.01$) and was highest in *Carya* [mean = 0.01,331 (SE = 0.00151)] and *Liriodendron* [mean = 0.01118 (SE = 0.00166)] and lowest in *Acer* [mean = 0.00302 (SE = 0.00037)] and *Fagus* [mean = 0.00217 (SE = 0.00037); Fig. 1a]. Mean *Quercus* biomass was 0.00623 (SE = 0.00071; Fig. 1a).

We detected Lepidoptera on 140 samples and the presence ranged from 7 to 36% among tree genera (Table 1), including all samples (n =626) or only samples with Lepidoptera (n = 140) in models produced similar results. Lepidopteron biomass varied by tree genus (P < 0.01) and was highest in *Carya* [mean = 0.00537 (SE = 0.00118)] and *Liriodendron* [mean = 0.00412 (SE = 0.00080)]; similar between *Acer* [mean = 0.00178 (SE = 0.00055)] and *Quercus* [mean = 0.00208 (SE = 0.00046)]; and lowest in *Fagus* [mean = 0.00094 (SE = 0.00053); Fig. 1b].

Fig. 1 Mean estimates with standard errors of total arthropod biomass (g/m; **a**), Lepidopteron biomass (g/m; **b**), arthropod guild diversity (H'; **c**), and arthropod guild richness (**d**) among dominant tree genera in the Shawnee National Forest, USA 2014
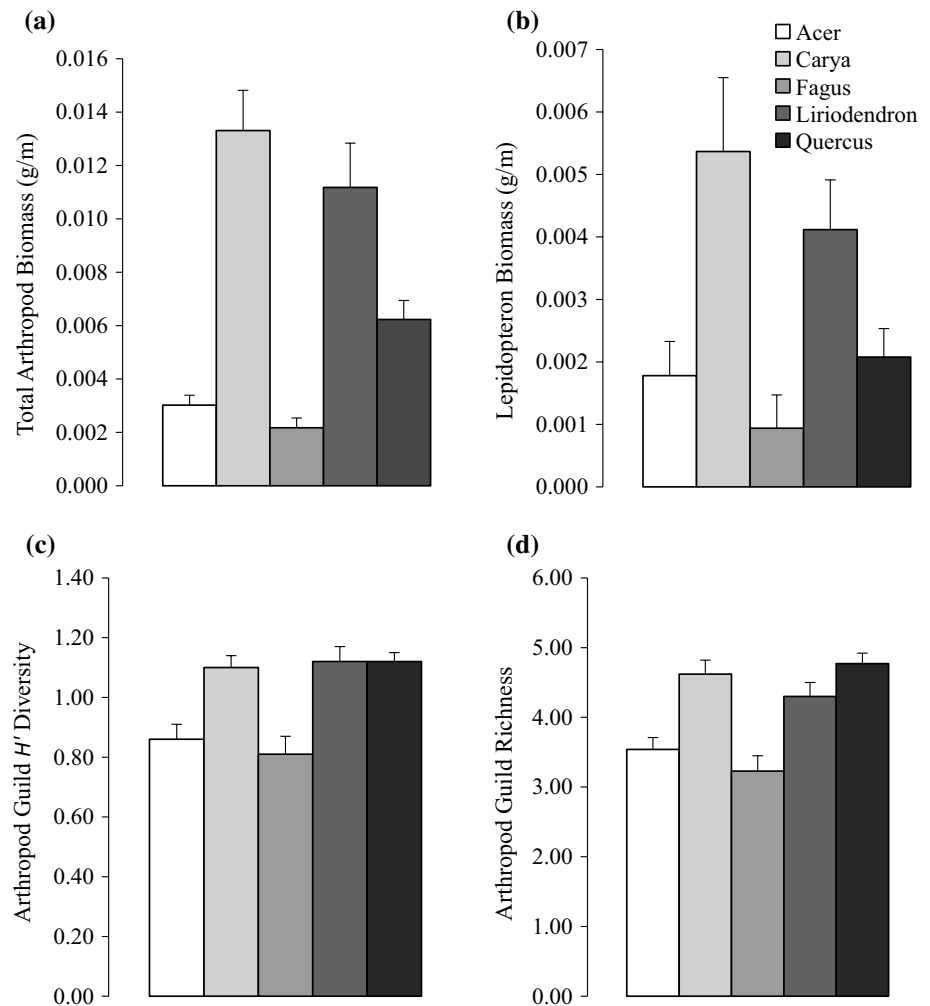
We used dry biomass of each guild divided by the total biomass of all guilds as an estimate of relative abundance. Arthropod guild Shannon diversity varied by tree genus ($P < 0.01$) and was highest in *Carya* [mean = 1.10 (SE = 0.04)], *Liriodendron* [mean = 1.12 (SE = 0.05)], and *Quercus* [mean = 1.10 (SE = 0.03)]; and lowest in *Acer* [mean = 0.86 (SE = 0.05)] and *Fagus* [mean = 0.81 (SE = 0.06); Fig. 1c].

Arthropod guild richness varied by tree genus (P < 0.01) and was highest in *Carya* [mean = 4.62 (SE = 0.20)], *Liriodendron* [mean = 4.30 (SE = 0.20)], and *Quercus* [mean = 4.77 (SE = 0.15)]; and lowest in *Acer* [mean = 3.54 (SE = 0.17)] and *Fagus* [mean = 3.23 (SE = 0.22); Fig. 1d].

Inconsistent with our second prediction, our results did not indicate that the overall arthropod biomass ($P = 0.11$) or Lepidopteron biomass ($P = 0.28$) varied significantly on host trees with the surrounding tree community. Alternatively, both arthropod guild Shannon diversity H' ($P < 0.01$, $\beta = -0.0953$) and guild richness ($P < 0.01$, $\beta = -0.5633$) decreased as % non-oak/hickory increased; however, the relationship between % oak/hickory and diversity ($P = 0.08$)

and % oak/hickory and richness ($P = 0.09$) interacted with tree genus at a marginally significant level. Therefore, we tested for relationships between tree genus and % oak/hickory for each genus separately. Arthropod guild Shannon diversity decreased with % non-oak/hickory composition for *Fagus* ($P = 0.02$, $\beta = -0.1679$) and *Quercus* ($P = 0.08$, $\beta = -0.0998$), and increased with % non-oak/hickory composition for *Carya* ($P = 0.05$, $\beta = 0.2084$); results were not significant for the other genera (Fig. 2). Arthropod guild richness decreased with % non-oak/hickory composition for *Acer* ($P = 0.02$, $\beta = -0.5755$), *Fagus* ($P < 0.01$, $\beta = -0.7470$), and *Quercus* ($P = 0.08$, $\beta = -0.0998$); results were not significant for other genera (Fig. 3).

Discussion

Anthropogenic stabilization of the environment has modified landscape-level plant communities worldwide (Livingston et al. 2016; Chudomelová et al. 2017; Stambaugh et al. 2017). An example of an anthropogenic impact that
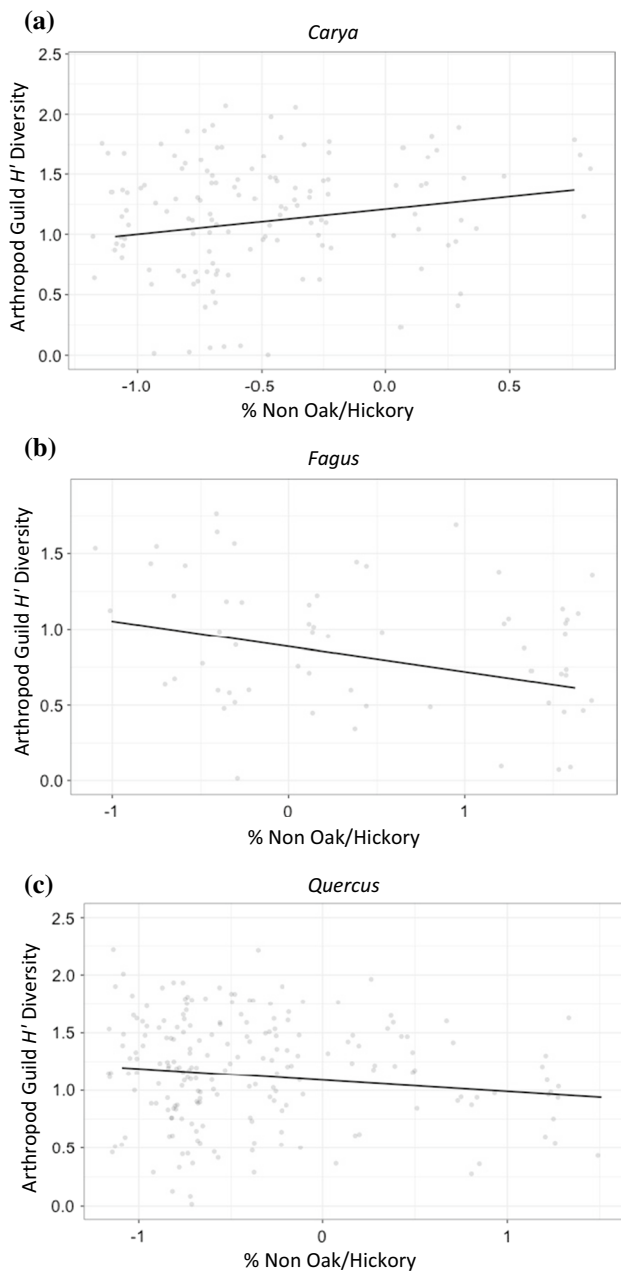
Fig. 2 Relationship between arthropod guild diversity H' on genus-specific host trees and % non-oak/hickory composition (standardized) of the surrounding forest landscape. The x axis represents the increasing percentage of non-oak/hickory. Relationships were statistically significant for *Carya* ($P = 0.05$, $\beta = 0.2084$, **a**), *Fagus* ($P = 0.02$, $\beta = -0.1679$, **b**), and *Quercus* ($P = 0.08$, $\beta = -0.0998$, **c**)

Fig. 3 Relationship between arthropod guild richness on genus specific host trees and % non-oak/hickory composition (standardized) of the surrounding forest landscape. The x axis represents the increasing percentage of non-oak/hickory. Relationship was statistically significant for *Acer* ($P = 0.02$, $\beta = -0.5755$, **a**), *Fagus* ($P < 0.01$, $\beta = -0.7470$, **b**), and *Quercus* ($P = 0.08$, $\beta = -0.4934$, **c**)

has modified plant composition among a variety of biomes is fire suppression (Donovan and Brown 2007; Burkle et al. 2015; Hessburg et al. 2015). Understanding how these modifications to plant communities influence higher trophic organisms will be critical for understanding the extent and potential for remediation of these landscape-level changes (Perring et al. 2015). Lack of disturbance in the eastern
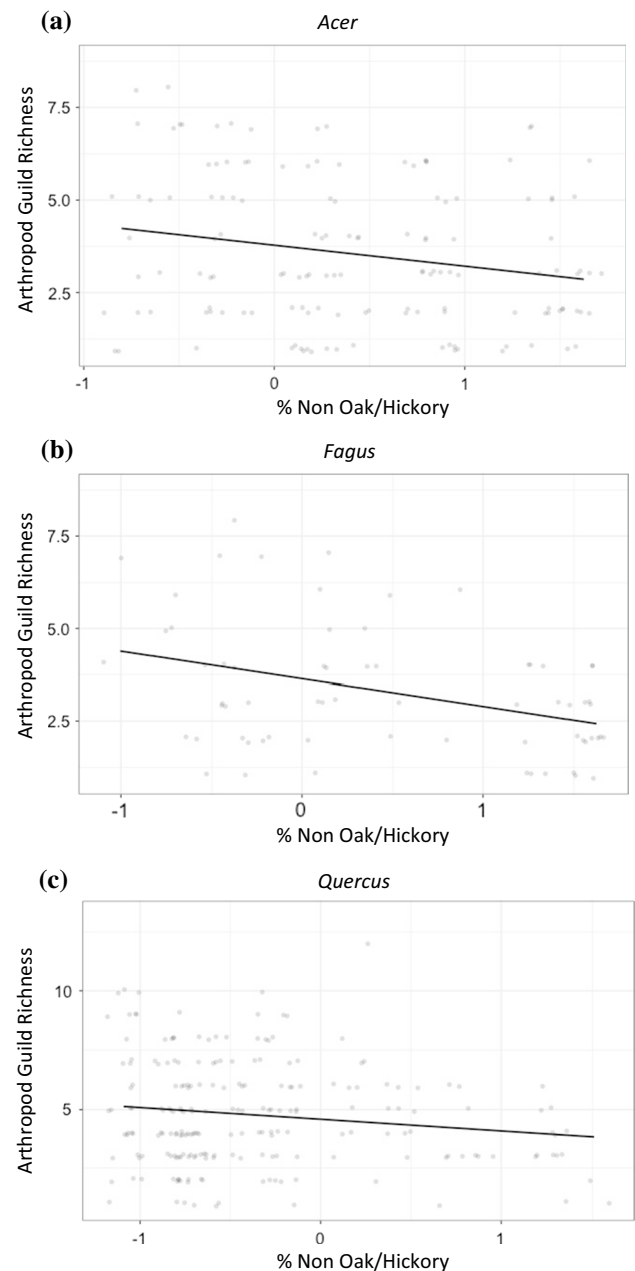
United States leads to a large-scale transition in forest composition from a mosaic of mid- and late-successional xeric and mesic communities to predominantly late-successional mesic communities (Nowacki and Abrams 2008; Fralish and McArdle 2009). Relationships among successional stage of forest community, growth rate, and shade tolerance of trees composing later successional forest communities, and their

level of chemical defense are becoming well established (Schuman and Baldwin 2016). These results led us to predict that foliage from slower growing, shade-tolerant tree species that historically dominated mesic ravines in eastern deciduous forests, but are now establishing on xeric slopes and ridge-tops due to lack of natural disturbance and past land usage, will support lower arthropod biomass, guild Shannon diversity, and guild richness.

Our results were consistent with this hypothesis; oak and hickory species contained more total arthropod biomass, Lepidopteron biomass, and guild Shannon diversity and guild richness per twig length unit than late-successional species (Fig. 1). We found the largest differences in biomass estimates between hickories and beech; hickories yielded estimates of almost an order of magnitude larger than beech. The level of investment into chemical defense and the influence of chemical compounds on leaf palatability likely explain the mechanism behind differences in arthropod biomass and community diversity among tree genera in our study. Multiple theories have been proposed as to why greater chemical defenses occur within slower-growing, shade-tolerant species (Stamp 2003). These theories are consistent in that they predict faster-growing, less shade-tolerant trees that compose earlier succession forest communities contain fewer chemical defenses relative to slower-growing, shade-tolerant species indicative of later successional communities.

Palatability of foliage, determined by the level of chemical and physical defenses for oaks, maples, and beech, is relatively well studied (Futuyma and Gould 1979; Summerville et al. 2003a, b). Although some species-specific variation exists, these variations can be predicted based on relationships between growth rate, shade tolerance, and arthropod palatability. For example, because of their faster growth with different and potentially fewer chemical defenses relative to later successional species, oaks tend to support high arthropod abundance and diversity, including high species richness of Lepidoptera (Butler and Strazanac 2000; Summerville et al. 2003b). Alternatively, foliage of beech trees appears to be one of the least palatable eastern hardwoods followed by most species of maple and then oaks (Brändle and Brandl 2001; Sobek et al. 2009).

We were able to locate relatively little information regarding the foliar chemical defenses or palatability of foliage from hickories and tulip tree. Hickory species compose as much as 30% of the tree community in oak/hickory forests and have similar levels of shade tolerance as oaks, but the species found in our study grow at a slower rate relative to oaks (Braun 1950). The little data available suggest that hickories have few allelochemicals relative to other trees and are of intermediate preference as forage by gypsy moths (Babosa and Krischik 1987). For this reason, we expected hickories to support lower biomass and diversity of arthropods relative to oaks, though higher than beech and maple. We observed, however, that hickory foliage supported greater arthropod and Lepidopteron biomass and similar arthropod guild Shannon diversity and guild richness metrics relative to oaks. On the surface, these results appear somewhat contradictory to Barbosa and Krischik (1987). The apparent contradiction, however, is explained by the possibility that gypsy moths may not be a good indicator of general arthropod or Lepidoptera palatability. Barbosa and Krischik (1987) also concluded that foliage of trees in the genus *Fagu*s was the preferred forage for gypsy moths, while tulip poplar was not favored. This result also contradicts what we and others observed for arthropods and more specific Lepidoptera (Heiermann and Schültz 2008). Although it is unclear as to why hickory foliage supports such high arthropod biomass, our results clearly indicate that hickories may be as important as or even more important than oaks as a platform for supporting arthropods as forage for secondary consumers in the oak/hickory forest community.

Tulip tree response provided intriguing results. It is a pioneer species that can tolerate only a limited amount of shading and grows faster than most mid- or late-successional tree species. Tulip tree is able to maintain a substantial presence, however, in more mature later successional forests (Wallace and Dunn 1980; Clebsch and Busing 1989). Tulip tree is chemically well-defended relative to many other species (Manuwoto et al. 1985), which is somewhat unexpected based on their intolerance to shade and fast growth. The foliage, however, is considered acceptable forage by a number of Lepidoptera larvae (Manuwoto et al. 1985). Furthermore, during colonization and while maintaining stand persistence, tulip tree is likely susceptible to arthropod invasion from a variety of arthropod generalists within highly diverse stands; therefore, multiple arthropod specialists likely evolved to tolerate its toxins (Feeny 1976). Consistent with this interpretation, we observed tulip tree to support arthropod and Lepidoptera biomass, guild Shannon diversity, and guild richness at a level above oaks and near that supported by hickories. This result suggests that forest communities undergoing mesophication but maintaining a substantial component of tulip tree may continue to benefit secondary consumers relative to those that do not.

Associational resistance occurs when host species are surrounded by less palatable or more diverse plant species (Root 1973; Castagneyrol et al. 2013). Thus, the process of mesophication has the potential to not only reduce the number of trees that support high abundance and diversity of arthropods, but associational resistance combined with this change in the tree community may compound the effect by reducing the abundance and diversity of arthropods on the more palatable trees remaining in the landscape.

Our results were only partially consistent with the hypothesis that associational resistance influences arthropod

abundance, diversity, and richness on host trees in eastern deciduous forests. We did not find evidence that arthropod abundance on host trees was influenced by plant composition of the surrounding landscape. It is possible that although individual beech and maple trees support a lower abundance of arthropods, tulip tree, which supports a high abundance of arthropods and provides as much as 60% RBA in some study sites, may have reduced differences in resource abundance between oak/hickory and non-oak/hickory communities to the point at which a difference in biomass was not detectable. The resource concentration hypothesis most often is invoked as the mechanism for explaining associational resistance when herbivores are specialists (Barbosa et al. 2009); in our case, the majority of herbivores were polyphagous generalists. Previous studies involving more complex plant communities such as ours have produced inconsistent results, and the relationship between associational resistance and stand diversity is much more tenuous when the herbivores are polyphagous (Barbosa et al. 2009).

As we predicted, there were negative relationships between arthropod community composition (i.e., guild Shannon diversity and guild richness) on host trees and prevalence of non-oak/hickory in the surrounding landscape within our study area. We detected declines in arthropod guild Shannon diversity and arthropod guild richness for all host tree genera except hickory (increase in diversity, Fig. 2a) when the host tree was located in non-oak/hickory sites. Differences were significant in arthropod guild Shannon diversity for beech, hickory, and oak; and in arthropod guild richness for maple, beech and oak (Figs. 2, 3). Either resource concentration, enemy abundance, or plant apparency may have reduced arthropod guild Shannon diversity and guild richness on these host trees (Andow 1991, Dulaurent et al. 2012). We believe that the enemies hypothesis can be disregarded as a potential mechanism because it is unlikely that non-oak/hickory sites supported more enemies than the oak/hickory sites. Invertebrate parasites and predators are thought to be more prevalent when more diverse vegetation provides greater structure (Root 1973). Additionally, avian predators are frequently found to influence arthropod abundance (e.g., Marquis and Whelan 1994, Strong et al. 2000). Within a concurrent study, both avifauna density and physical structure of the forest plant community were greater in oak/hickory sites (Sierzega 2016). This suggests that if herbivorous arthropod predators varied among landscapes, they were greater in oak/hickory sites (Sierzega 2016). Similarly, because all host trees in our study were surrounded by a diverse composition of neighbors and plant structure was greater in oak/hickory sites (Sierzega 2016), it is unlikely that host tree apparency was lower in the non-oak/hickory sites. The more likely explanation for lower estimates of arthropod guild Shannon diversity and guild richness in non-oak/hickory mesic sites from our study is the difference in nutrient availability between these forest types. We observed significantly greater biomass on individual oak and hickory sample trees, suggesting that these species provide high levels of nutrients or are less well defended from herbivores (Forkner and Hunter 2000, Zehnder et al. 2010). We suggest that landscapes dominated by tree genera in which nutrient resources are more concentrated (e.g., oaks and hickories) allow for a more diverse and species-rich herbivore community. Greater biodiversity is associated with greater ecosystem function and processes (Tilman et al. 2014). Moreover, greater richness and diversity of arthropods may allow for greater environmental function and resilience (Naeem et al. 2012; Tilman et al. 2014). Therefore, a more diverse arthropod community should better withstand the predicated greater annual climatic variation associated with climate change (Lunt et al. 2013).

Hickory samples were unique in that they indicated a slightly positive relationship between arthropod guild Shannon diversity and % non-oak/hickory in our study. The only explanation we can provide for this lack of congruency between hickory and the other genera is an artifact of our sampling process. In our sample, we did not have host trees from the genus *Carya* in sites that were extremely (< − 1) non-oak/hickory dominated (Figs. 2, 3). Thus, our ability to detect a decline is arthropod diversity or richness as mesophication ensues is limited.

Legacy effects from logging, mining, and natural disturbances have been proposed to explain heterogeneity in the species composition of arthropod communities among forest stands in second growth forests of North America (Holl 1996; Summerville et al. 2009; Schowalter et al. 2017). Summerville et al. (2009) found potential legacy effects > 60 years after the completion of logging. Our results are consistent with the paradigm that variation in disturbance types is associated with variation in the species composition of the tree community dominating the disturbed area (Hunter and Price 1992; Summerville and Crist 2008). This variation in tree communities, in turn, influences the species composition of the arthropod community dependent on these trees.

Lower arthropod biomass on maples and beech and lower arthropod guild Shannon diversity and guild richness in non-oak/hickory sites from our study are concerning, as these species will likely reach canopy dominance as mesophication ensues in the continued absence of disturbance (Nowacki and Abrams 2008). Although inference from our study is limited to our study system, anthropogenic modifications to disturbance regimes have impacted species composition of a variety of biomes worldwide (Chudomelová et al. 2017, Stambaugh et al. 2017). As demonstrated by our results, these modifications to disturbance regimes may not only directly impact composition and diversity of primary producers, but may also indirectly impact abundance

and diversity of higher trophic organisms (Hunter and Price 1992, Mori et al. 2013, Perring et al. 2015). More studies describing how anthropogenic-induced modifications to disturbance regimes will be required if we are to fully understand and mediate impacts and maintain organismal diversity.

Author contribution statement KS helped develop and design the study, collected and analyzed the data, helped interpret the results and drafted the original article; ME developed and designed the study, helped interpret the results, substantially edited the original draft and created the final draft.

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