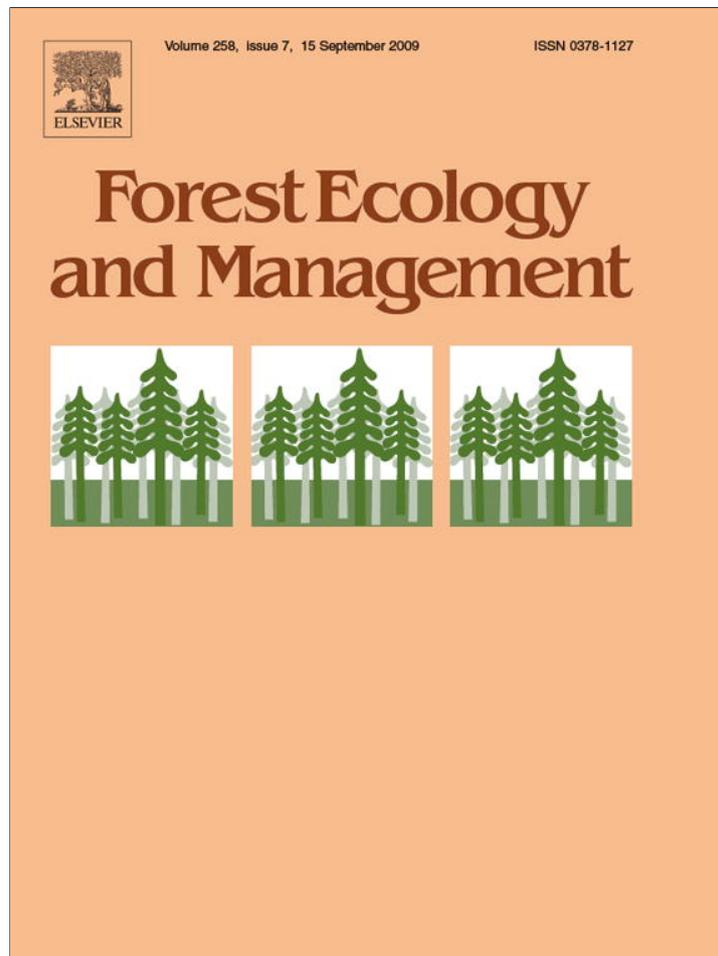


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Response of arthropod biodiversity to foundation species declines: The case of the eastern hemlock

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ABSTRACT

Widespread declines of foundation species, such as many corals, kelps, and overstory trees, are of grave concern because, by definition, these species create and maintain habitat that supports other species. Nevertheless, past responses to their declines, many of which were caused by invasive species, have been late and ineffective, underscoring the need to predict changes in biodiversity and ecosystem function associated with species invasions and foundation species losses. One predictive, but under-used, approach is to compare the species and functions associated with the afflicted foundation species to its projected replacement communities. The taxa associated with the foundation species and subsequent successional stages would be expected to decline and increase, respectively. We used this approach to generate hypotheses for how arthropod diversity might change in response to extensive losses of eastern hemlock trees caused by the invasive, hemlock woolly adelgid (insect: Hemiptera, Adelgidae). Our all-strata survey of the arthropods in an eastern hemlock forest and its expected replacement climax community in the mid-Atlantic region of the United States, mixed hardwood forest, suggests that eastern hemlock losses might initiate increases in arthropod abundance, alpha diversity, and 23 arthropod taxa, might produce no change in evenness or composition of arthropod functional groups, but might trigger decreases in beta diversity and seven hemlock indicator taxa. These predictions are consistent with observed trends in arthropod responses to hemlock losses in other studies, and thus might be useful for targeting early monitoring, management, and conservation efforts. This research is exploratory, however, and tests of these predictions across larger spatial scales will be necessary to determine the generality of the findings.

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1. Introduction

Foundation species are species that define much of the local community structure by creating stable conditions for other species and by modulating ecosystem processes (*sensu* Dayton, 1972; Ellison *et al.*, 2005a). Many foundation species, such as numerous overstory trees, corals and kelp, have experienced or are experiencing widespread declines, most of which are at least partly driven by invasive pests and pathogens (Ellison *et al.*, 2005a). For instance, in North America chestnut blight and Dutch elm disease have nearly eliminated the American chestnut and American elm, two foundation tree species (Lovett *et al.*, 2006), and countless coral species are being threatened by a variety of diseases (Harvell *et al.*, 1999).

Declines of foundation species typically necessitate urgent conservation action because, by definition, these species establish and maintain habitats that support other species (Ellison *et al.*, 2005a); thus their losses pose grave risk of secondary species declines (Ebenman and Jonsson, 2005). In spite of this risk, our past response to foundation species losses has often been too late and ineffective (Ellison *et al.*, 2005a). Even in cases where we could not or cannot stop a species invasion or a foundation species loss, it is plausible that by understanding the post-invasion or post-decline trajectory of the ecosystem we could minimize the resulting consequences, such as secondary species declines. Hence, a shift from a historically reactive approach to one where we generate defensible hypotheses for how biodiversity and ecosystem function will change with declines of foundation species should facilitate appropriately targeting early monitoring, management, and conservation efforts.

Predicting responses to foundation species declines requires understanding (1) the successional processes following foundation species losses and (2) the species and functions generally

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associated with the afflicted foundation species and subsequent successional stages. Specifically, declines of foundation species might cause secondary declines of taxa and ecosystem functions positively associated with the afflicted foundation species. Conversely, there should be increases in those taxa and functions that are positively associated with the succeeding species. Finally, the magnitude of these changes should be proportional to the strength of the association between the taxa/function and the foundation and succeeding species. While this predictive and comparative method is not novel, it has not been thoroughly embraced as a proactive approach to species invasions and foundation species declines (but see Ellison et al., 2005b).

We used this comparative technique and associated statistical methods to predict changes in arthropod diversity and function associated with the decline of eastern hemlocks (*Tsuga canadensis* L. Carrière), a foundation tree species in eastern North America (Ellison et al., 2005a; Lovett et al., 2006). Losses of eastern hemlock have been predominantly caused by a highly virulent, invasive, aphid-like pest, the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand; McClure, 1990; Orwig and Foster, 1998), that could eliminate most eastern hemlocks from North American forests in the next half century (Orwig et al., 2002; Ellison et al., 2005a).

When possible, predictions of community responses to species invasions and foundation species declines should be based on the majority of biodiversity and should emphasize taxa that are threatened and important to ecosystem functions. These criteria led us to generate hypotheses for how arthropod diversity will change with hemlock declines. Arthropods drive many vital ecosystem functions and services and represent the majority of multicellular diversity in most ecosystems (Kremen et al., 1993; Samways, 2005). Further, arthropods are poorly studied in most habitats (Dunn, 2005) and often make up a substantial portion of the most threatened species (Kim, 1993; Goldstein, 2004). Indeed, most past and predicted extinctions are of insects (Dunn, 2005).

We compared the arthropod biodiversity in a hemlock forest of Shenandoah National Park (VA, USA; a HWA-afflicted region) to the arthropod biodiversity associated with their expected replacement climax community. Although black birch has repeatedly been suggested to benefit most from hemlock mortality (Orwig and Foster, 1998; Stadler et al., 2005), this species is likely to be replaced by a climax community of more shade tolerant hardwood species (Mahan et al., 2004b; Lovett et al., 2006). This assertion is supported by long-term data (Jenkins et al., 1999; Orwig et al., 2002; Mahan et al., 2004b; Small et al., 2005), and a spatially explicit, stem-based succession model (Jenkins et al., 2000). Hence, we compared the arthropod communities of hemlock forest to nearby mixed hardwood forest containing beech, birch, oaks, and maples. We focused on the post-hemlock climax community because it is the successional stage that is most likely to exemplify stable, long-term effects that tend to be superior to acute effects for predicting ecological and economic consequences of human-induced change (Strayer et al., 2006). Given that it can take at least a half century to reach a climax community, it would be valuable to understand the biodiversity of the transitional stages; such an effort is, however, beyond the scope of our current study.

Our first objective was to compare the arthropod abundance, richness, and evenness of hemlock and hardwood forests to engender hypotheses for how abundance and alpha and beta diversity will respond to the expected hemlock to mixed hardwood succession. Our second objective was to identify taxa whose associations with these forest types were greater than expected by chance so we could hypothesize specific changes in structural diversity. Finally, we set out to compare the distribution of arthropods among functional groups (feeding guilds) so we could hypothesize how functional diversity will be affected by hemlock losses.

2. Materials and methods

2.1. Background on system

HWA was first introduced into Virginia from Japan in the 1950s, spread rapidly, but did not begin causing severe mortality of eastern hemlocks until the 1980s (Lovett et al., 2006). HWA feeds on the phloem of hemlock twigs typically causing tree death within five years (McClure, 1991; Young et al., 1995). Infestation intensity and induced hemlock mortality tends to decline with increasing latitude (Orwig et al., 2002). In certain regions of the southern United States, HWA has killed 92% of the hemlocks within 15 years (Bair, 2004). In Connecticut, declines have been less pronounced, but even there HWA has killed hemlocks of all size- and age-classes (Orwig, 2002; Orwig et al., 2002). There is also no evidence of resistance or recovery from HWA infestations (Orwig and Foster, 1998) and as yet no effective means for controlling HWA at the stand or ecosystem level (Wallace and Hain, 2000; Lovett et al., 2006).

Eastern hemlocks create and maintain a distinct habitat of deep shade, acidic and nutrient-poor soils, moist and cool microclimate, and slow litter decomposition and nitrogen cycling. There is growing evidence that this habitat supports a unique assemblage of species (Jenkins et al., 1999; Snyder et al., 2002; Tingley et al., 2002; Ross et al., 2003; Ellison et al., 2005b; Dilling et al., 2007) and ecosystem functions (Jenkins et al., 1999; Kizlinski et al., 2002; Stadler et al., 2005, 2006), raising concerns regarding the presumed functional loss of hemlocks from eastern North America. Nevertheless, a thorough understanding of species associations with hemlock forests versus other forest types has yet to be attained.

2.2. Sampling approach

We conducted our study at Shenandoah National Park in the mid-Atlantic Appalachian Mountains of Virginia. We used the general sampling design of Young et al. (2002) to assess biodiversity in hemlock and hardwood forests. Hemlock and mixed hardwood sites were selected based on multivariate distance of landscape attributes (using a 1:24,000 digital elevation model) so that sites had a first-order stream and similar elevation, slope, stand size, and perimeter (hemlock: 973 m, 7.0°, 39.8 ha, 8571 m; hardwood: 830 m, 8.9°, 29.8 ha, 5022 m; respectively). The hemlock stand was >120 years old while the hardwood stand was approximately 70 years old. We intentionally picked hemlock sites that had not been infested by HWA so we could quantify a relatively pristine hemlock community. Given the intentional similarities between these stands and the rare presence of hemlocks in the hardwood stand and the presence of hardwoods in the hemlock stand (see Section 3), it seems likely that both sites could support hardwood and hemlock species.

Many studies focus on a small number of arthropod families facilitating species-level identification because of the associated limited taxonomic scope. However, the risk of focusing on a small number of families is missing the taxa most sensitive to the stressor(s) of interest. Further, it is unrealistic to manage and monitor most arthropods at the species level due to the lack of funds, time, and expertise for non-pest-related arthropod research (Rohr et al., 2007). Hence, our emphasis was on the taxonomic breadth that is often lacking in many arthropod conservation studies and thus we focused on sampling “all arthropods” and minimally identifying our specimens to the family level. Funds were acquired to send specimens to taxonomic specialists for genus- and species-level identification (i.e. taxonomic depth) whenever specialists were available and willing to accept specimens (see list in Mahan et al., 2004a). However, taxonomic specialists were inarguably a limited resource (see Section 4).

Table 1

Type and number of collection methods used in the inventory of arthropods in the three strata of the sampled hemlock and hardwood forests of Shenandoah National Park (USA), 1997.

Collection	Strata	Samples per forest type
Pitfall	Soil	11
Leaf litter sample	Soil	15
Soil core	Soil	15
Substrate search	Soil	10
Beat sheet	Understory	5
Malaise trap	Understory	6
Lower branch clip	Understory	6
Sweep net	Understory	3
Tree trunk trap	Understory	5
Malaise trap	Canopy	2
Upper branch clip	Canopy	6
Total		84

We established 16, 20 m × 20 m plots in each of the two forest types. The plots were 25 m apart, 15 m from a first-order, and 100 m from the headwaters of the stream, and we used 11 invertebrate collecting methods distributed across the three forest strata (soil, understory, and canopy) in the plots (Mahan et al., 2004a). Each collecting method was assigned to one specific stratum, and collecting methods were distributed randomly among the plots (Table 1; Rohr et al., 2007). Within each plot, soil-based collecting was conducted 5 m from the plot center in a randomly selected direction; vegetation-based collecting methods were conducted on a randomly selected tree or shrub in each plot; and ground malaise traps were placed in light gaps and potential arthropod flyways. Each sampling method was applied identically to each plot. Details on the size of soil cores, time constraints for substrate searches, how leaf litter samples were taken, height and length of branch clips, methods for sweep netting, etc., are provided in Mahan et al. (2004a). Overstory tree composition was also quantified as stem density in four randomly selected plots within each forest type.

Parataxonomists, trained in entomological techniques, conducted the all-arthropod field sampling and specimen identification to the family and morphospecies levels. Acari, Pseudoscorpiones, and Protura were the only arthropod orders not identified to family, and these three orders plus classes Collembola, Julida, Lithobiomorpha, Neuroptera, and family Cecidomyiidae (Diptera) were the only taxa not identified to morphospecies. All families were assigned a feeding guild (detritivorous, herbivorous, omnivorous, zoophagous) based on the adult feeding behavior of the majority of species in the family (according to diet information provided by Borror and De Long, 1970). This is admittedly just an estimate of the feeding guild given that larval and adult forms of the same species can occupy different feeding guilds and that a single insect family can contain species with a wide array of different feeding modes. All specimens were deposited in The Pennsylvania State University Frost Entomological Museum, University Park, PA. The taxonomic scope of the survey (most arthropod taxa) unfortunately came at the expense of temporal breadth, for the survey was only conducted in August 1997. This time of year was selected because the end of summer can have the greatest richness and abundance of terrestrial arthropods for temperate forests and thus likely captures the most arthropod diversity relative to other times of the year (Marquis and Whelan, 1994; Nakano and Murakami, 2001; Lill and Marquis, 2003; Summerville et al., 2003). The same type and number of collecting methods were employed each day in each forest to control for temporal confounders.

2.3. Statistical analyses

We first assessed whether the plots were statistically independent of one another (i.e. whether there was spatial

autocorrelation resulting in some level of pseudoreplication) by conducting a Mantel test to determine whether there was a significant relationship between distance among plots (based on Euclidean distance) and similarity of their epigeal arthropod communities (based on a Bray-Curtis index; 999 iterations). We then used a generalized linear model with a Poisson error distribution and an overdispersion parameter to test whether arthropod abundance differed between the forests. To control for heterogeneity among plots within forests in this analysis, we conducted a paired test. Plots were first ranked within each forest based on their arthropod abundances and then plots between the two forests were paired based on these abundance rankings.

To predict changes in alpha diversity associated with hemlock declines, we compared the arthropod richness and evenness of the forests. To control for unintentional sampling biases that can occur even when sampling type and number are identical among habitats (Gotelli and Colwell, 2001), we compared the number of arthropod families in each forest at a standardized number of individuals sampled using individual-based rarefaction curves and “true” or asymptotic richness estimates (Gotelli and Colwell, 2001). Individual-based rarefaction curves are predicted taxa accumulation curves (based on the mean of 50 randomizations of sample order) plotted as a function of accumulated individuals (Gotelli and Colwell, 2001). We used the statistical program EstimateS 7.0 (Colwell, 2005) to interpolate the arthropod rarefaction curve for the “most-family-dense” habitat (the forest with more families at the maximum number of samples; in our case, the hardwood forest) so that the two forests were compared at the maximum number of individuals collected in the “least-family-dense” forest (Gotelli and Colwell, 2001). Because taxa evenness comparisons are also influenced by the same biases as comparisons of taxa counts, analogous procedures were used to interpolate and compare taxa evenness [characterized using Hurlbert’s probability of an interspecific encounter] using Ecosim 7.0 (Gotelli and Entsminger, 2001). We compared the “true” or asymptotic richness of the two forests with Michaelis–Menten, ICE and Chao2 richness estimators also obtained using EstimateS 7.0 (Colwell, 2005). We compared the forests using three extrapolation techniques because there can be substantial variation in the true richness estimates among extrapolation methods. Michaelis–Menten extrapolation uses the Michaelis–Menten function to estimate the asymptote for richness and is thus an analytical approach. The ICE and Chao2 estimators use the number of uniques and duplicates (families that occur in only one or two samples, respectively) or singletons and doubletons (families represented by only one or two individuals, respectively) to estimate the number of families that were not sampled. This is then coupled with the number of families that were collected to estimate the true family richness. Probability values for richness and evenness comparisons were calculated using Z-tests (recommended by Gotelli and Entsminger, 2001).

To predict changes in beta diversity associated with the expected hemlock to mixed hardwood succession, we compared taxonomic similarity of samples between forest types to the taxonomic similarity of samples within the hardwood forest (at the family level). If similarity within the hardwood forest is greater than the similarity between the hemlock and hardwood forests, then succession from hemlock to mixed hardwood forest should reduce beta diversity. Jaccard (incidence-based) and Bray-Curtis (abundance-based) dissimilarity indices were calculated for pairwise comparisons of samples using EstimateS 7.0 (Colwell, 2005). To ensure that our sample size was not inflated by the multiple pair-wise comparisons, we used a Monte Carlo permutation test (9999 iterations) to compare the within- to between-forest similarity measures.

To determine which taxa-habitat associations were greater than expected by chance, we conducted an “indicator species analysis” in PC-ORD (v. 5.01; McCune and Mefford, 1999), which follows the general guidelines of Dufrene and Legendre (1997). The indicator value of a taxon for a habitat is the product of its relative abundance (a measure of exclusiveness or concentration of abundance) and relative frequency (a measure of faithfulness or constancy of presence in a particular group) in that habitat multiplied by 100 (Dufrene and Legendre, 1997). To take advantage of the extensive but incomplete genus and species identification performed by taxonomic experts, we conducted these analyses on the lowest taxonomic level with ≥ 10 individuals in the database. The indicator analyses were based on the six forest-by-strata combinations, and Monte Carlo permutation tests, reassigning the sample units to these six groups 9999 times, were used to evaluate the significance of the indicator value for each taxon.

Finally, it is possible that any differences in community composition between the forests were accompanied by concomitant differences in the distribution of functional groups. If so, this might translate into changes in function, as well as structure, if mixed hardwoods replace hemlocks. To test this hypothesis, we conducted a MANOVA to assess whether there were differences between the forests in the percent of arthropod individuals (angular transformed) among the four feeding guilds. As with the

abundance analysis, plots for the guild analysis were paired by their rank abundance to minimize the impact of spatial heterogeneity within the forests (i.e. we blocked by the abundance rank of the 16 plots).

3. Results

The hemlock forest plots were dominated by eastern hemlocks (mean \pm SE: $71.2 \pm 3.8\%$ of individual overstory trees), followed by sweet birch ($11.6 \pm 2.7\%$), species of maple [red (*Acer rubrum*) and sugar (*Acer saccharum*); $6.5 \pm 2.8\%$] and oak [Northern red (*Quercus rubra*) and chestnut (*Q. prinus*); $3.6 \pm 2.5\%$], and white ash ($3.1 \pm 2.2\%$). The mixed hardwood plots were comprised predominantly of oak species [Northern red (*Q. rubra*), chestnut (*Q. prinus*) and black oak (*Q. velutina*); mean \pm SE: $33.2 \pm 10.3\%$ of individual overstory trees], maple species [red (*A. rubrum*) and striped maple (*A. pennsylvanicum*); $20.2 \pm 4.9\%$], birch species [sweet (*Betula lenta*) and yellow birch (*B. alleghaniensis*); $12.1 \pm 7.8\%$], and white ash (*Fraxinus americana*; $9.6 \pm 3.2\%$), but no eastern hemlock.

We collected 8636 arthropods that represented 29 arthropod orders. Twenty-six of the 29 arthropod orders were identified to the family level, resulting in 167 families collected in our study. In both forests, the soil layer was dominated by mites and Collembolans and the understory and canopy was dominated by true flies (Fig. 1). Detailed taxonomic lists and abundance data are

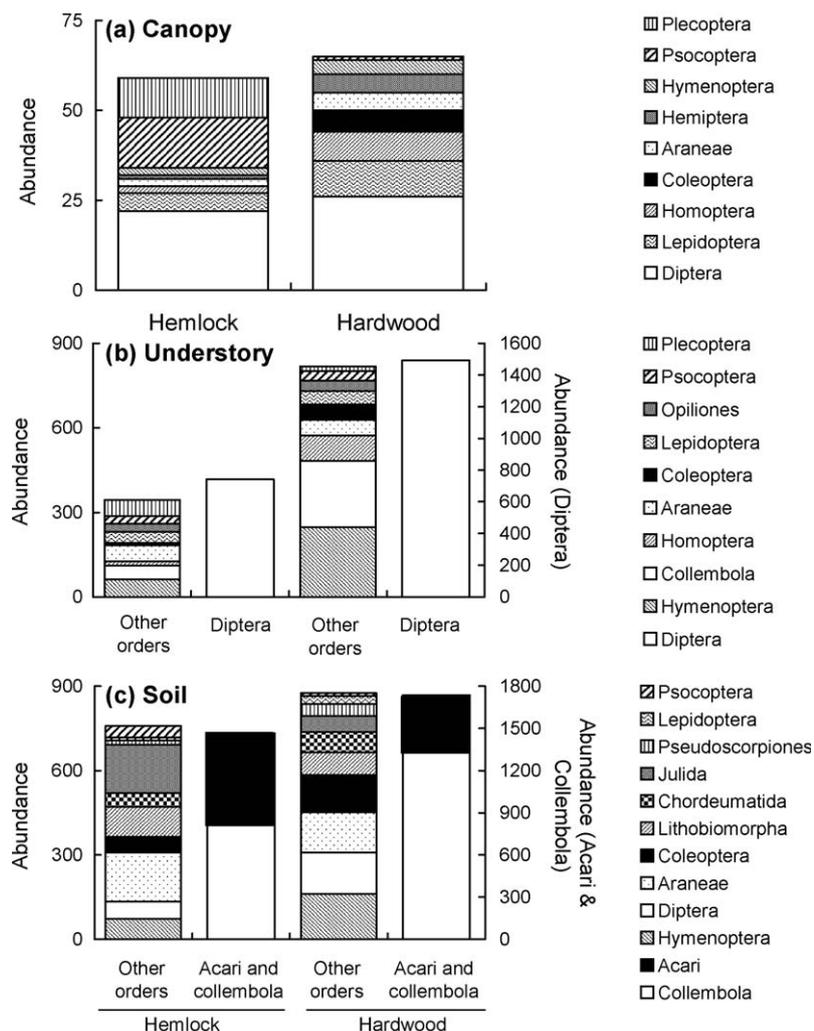


Fig. 1. Abundance of the most common arthropod orders in the (a) canopy, (b) understory and (c) soil strata of the sampled hemlock and hardwood forests of Shenandoah National Park (USA). For each forest, the figure displays greater than 90%, 97%, and 95% of the arthropods in the canopy, understory, and soil strata, respectively. Although order Homoptera has been moved into the order Hemiptera, we treat it as a separate order in this figure.

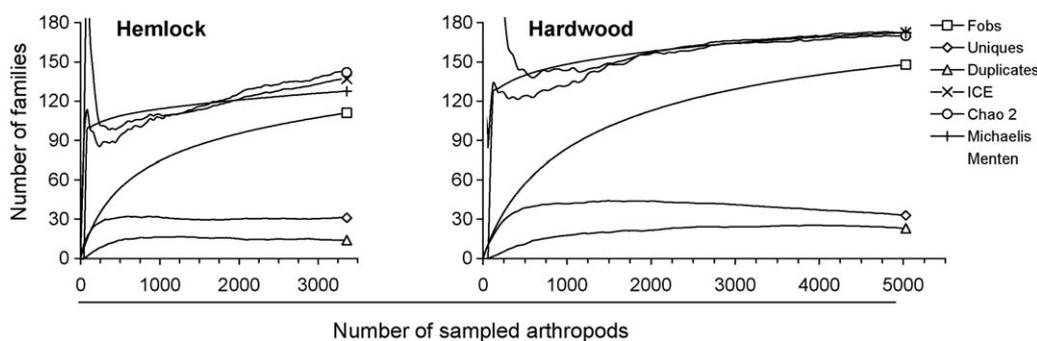


Fig. 2. Individual-based family rarefaction (Fobs = families observed), estimated true richness (ICE, Chao2, Michaelis–Menten, see Section 2 for description of these extrapolation methods), and uniques and duplicates (families in only one or two samples, respectively) curves for the sampled hemlock and hardwood forests of Shenandoah National Park (USA).

available in Mahan et al. (2004a). Although we had funds to pay taxonomic specialists to identify specimens to genus and species, this level of identification is incomplete largely due to a lack of available specialists. Despite the incomplete species-level identification, specialists documented three undescribed species that were found only in the hemlock forest (two Dipterans: *Orfelia* sp. and *Symmerus* sp., and one Hemipteran: *Cyrtolobus* sp.), and eight undescribed species that were found exclusively in the hardwood forest (Mahan et al., 2004a). We found no HWA or evidence of HWA damage in any plots.

The relationship between diversity and distance between plots within forests was not statistically significant (standardized Mantel $r < 0.215$, $p > 0.198$), suggesting that there was no spatial autocorrelation and that the plots were statistically independent samples. The generalized linear model analyses based on the Poisson error distribution (scaled deviance = 0.82) revealed that the hardwood forest had significantly more arthropod individuals than the hemlock forest (least squares mean \pm 1 SE: 56.63 ± 6.70 , 36.81 ± 6.70 arthropods; $Wald Stat_{1,15} = 72.93$, $p < 0.001$; Fig. 1). The individual-based arthropod rarefaction curves indicated that the hardwood forest had a larger decline in the rate of accumulated families per individual collected, and extrapolation estimates that were more independent of sampling effort (i.e. they tended to increase less with an increase in families; Fig. 2). These observations suggest that the hardwood forest was inadvertently sampled more intensively than the hemlock forest (likely due to hardwood forests being warmer than hemlock forests, a factor which would increase arthropod activity and encounters with our traps), emphasizing the importance of standardizing our comparison of these habitats by sampling effort (Gotelli and Colwell, 2001).

Controlling for this potential bias in sampling effort revealed that there were no detectable differences in evenness between the forests and that the hardwood forest had significantly greater interpolated and extrapolated family richness than the hemlock forest (Fig. 3a–d). Both the interpolation and extrapolation results suggested that the greatest difference in richness between the forests was in their soil layers (Fig. 3b–d). Indeed, if the hardwood forest replaces the hemlock forest, there would be an estimated 20% increase in overall alpha diversity and an estimated 48% increase in the alpha diversity of the soil stratum (Fig. 3a–d). As for beta diversity, samples within the hardwood forests were more taxonomically similar than samples between forests, regardless of whether these analyses were based on incidence data (least squares Jaccard mean \pm 1 SE: 0.237 ± 0.019 , 0.164 ± 0.019 , respectively, $p = 0.004$) or abundance data (least squares Bray–Curtis mean \pm 1 SE: 0.324 ± 0.021 , 0.196 ± 0.021 , respectively, $p = 0.001$).

The indicator taxa analysis revealed 23 taxa that were significant indicators of the hardwood forest and seven taxa that

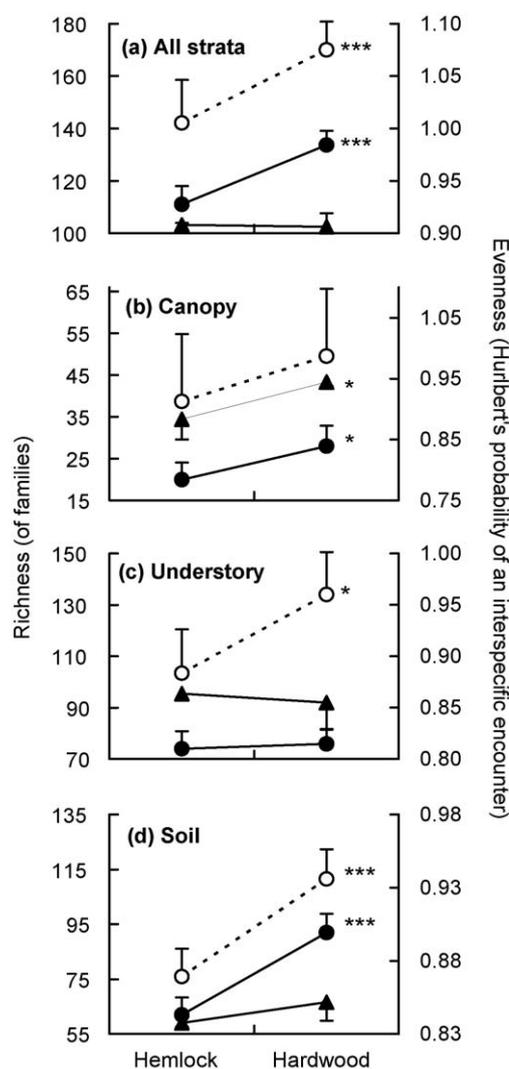


Fig. 3. Family richness (solid circles) and evenness (Hurlbert's probability of an interspecific encounter; triangles) estimates interpolated to the least family dense forest and extrapolated true richness estimates (using the Chao 2 estimator; open circles) for (a) all strata combined, (b) the canopy stratum, (c) the understory stratum, and (d) the soil stratum of the sampled hemlock and hardwood forests of Shenandoah National Park (USA). Interpolated richness and evenness were standardized to the total number of individuals in the less family dense forest at that stratum to control for differences in sampling effort (see Section 2 for details). Means and standard deviations (although some are too small to see) are displayed and statistical comparisons were made between forests using Z-tests. Standard deviations are only provided in one direction to reduce overlap of the error bars. * $p < 0.05$, *** $p < 0.001$.

Table 2
Results of “indicator species” analyses identifying the significant indicator taxa for the strata of the sampled hardwood and hemlock forests of Shenandoah National Park (USA), 1997.

Taxon ^a					Group		Indicator value (IV) randomized from groups ^b		Observed IV
Class	Order	Family	Genus	Species	Forest	Stratum	Mean	St. dev.	
Arachnida	Aranea	Lycosidae			Hardwood	Soil	7.3	5.03	21.6*
Arachnida	Opiliones	Sclerosomatidae	Leiobunum		Hardwood	Understory	9.9	5.42	25.9*
Insecta	Coleoptera	Staphylinidae			Hardwood	Soil	9.2	5.87	20.4*
Insecta	Diptera	Cecidomyiidae			Hardwood	Understory	12.4	6.47	30.8*
Insecta	Diptera	Ceratopogonidae	Atrichopogon		Hardwood	Understory	5.5	4.56	17.4*
Insecta	Diptera	Dolichopodidae	Dolichopus		Hardwood	Understory	6.3	4.67	20.0*
Insecta	Diptera	Dolichopodidae	Hercostomus		Hardwood	Understory	7.5	5.00	18.2*
Insecta	Diptera	Mucidae	Phaonia		Hardwood	Understory	7.0	4.96	24.1*
Insecta	Diptera	Muscidae	Coenosia		Hardwood	Understory	8.4	5.42	24.3*
Insecta	Diptera	Mycetophilidae	Tetragoneura		Hardwood	Understory	5.8	4.49	21.7*
Insecta	Diptera	Sciaridae			Hardwood	Understory	10.8	5.96	30.4*
Insecta	Diptera	Simuliidae	Simulium	jenningsi	Hardwood	Understory	5.8	4.61	21.7*
Insecta	Diptera	Sphaeroceridae			Hardwood	Understory	8.4	5.39	25.6*
Insecta	Diptera	Tipulidae	Tipula		Hardwood	Understory	6.7	4.56	21.0*
Insecta	Hemiptera	Aphididae			Hardwood	Canopy	8.8	5.34	18.9*
Insecta	Hemiptera	Cicadellidae	Morpho1		Hardwood	Understory	9.2	5.62	23.5*
Insecta	Hemiptera	Cicadellidae	Empoasca		Hardwood	Understory	6.2	4.73	20.4*
Insecta	Hymenoptera	Braconidae			Hardwood	Understory	7.4	4.98	29.6**
Insecta	Hymenoptera	Diapriidae			Hardwood	Understory	8.2	5.40	28.0*
Insecta	Hymenoptera	Formicidae	Aphaenogaster		Hardwood	Soil	8.2	5.46	27.5**
Insecta	Hymenoptera	Ichneumonidae			Hardwood	Understory	9.9	5.88	23.2*
Insecta	Lepidoptera	Noctuidae			Hardwood	Understory	10.2	5.65	32.9**
Insecta	Lepidoptera	Notodontidae			Hardwood	Canopy	6.7	4.80	46.0***
Arachnida	Acari				Hemlock	Soil	18.3	6.02	41.8**
Arachnida	Opiliones	Phalangiiidae	Odiellus	pictus	Hemlock	Understory	9.6	5.73	21.4*
Chilopoda	Lithobiomorpha	Lithobiidae			Hemlock	Soil	12.4	5.85	24.0*
Diplopoda	Julida	Parajulidae			Hemlock	Soil	13.2	6.92	31.7*
Insecta	Diptera	Mycetophilidae	Mycomya		Hemlock	Understory	7.9	5.32	23.6*
Insecta	Plecoptera	Leuctridae	Leuctra	ferruginea	Hemlock	Canopy	9.3	5.53	33.7**
Insecta	Plecoptera	Nemouridae	Amphinemura	wui	Hemlock	Understory	6.6	4.72	22.1*

^a We conducted the analyses on the lowest taxonomic level with ≥ 10 individuals in the database.

^b The indicator value is the product of the relative abundance and relative frequency of the taxon in that habitat multiplied by 100.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

were indicators of the hemlock forest (Table 2). The indicators for the hardwood forest were predominantly from class Insecta in the orders Diptera (flies), Hemiptera (aphids and leafhoppers), Hymenoptera (ant, bees, and wasps), and Lepidoptera (butterflies and moths). In contrast, the indicators for the hemlock forest were represented by a more even mix of classes which included Arachnida (mites, spiders, harvestmen), Chilopoda (centipedes), Diplopoda (millipedes), and Insecta.

Although there were compositional differences between the forests, we found no evidence that these differences were accompanied by differences in the distribution of their arthropods among adult functional groups. The detritivorous, herbivorous, omnivorous and predaceous feeding guilds were comprised of 35.86%, 35.78%, 6.88%, 21.48% of the arthropod individuals, respectively, but these percentages were not significantly different between the hemlock and hardwood forests (Wilk's $F_{4,12} = 0.80$, $p = 0.547$).

4. Discussion

By comparing the arthropod abundance, richness, evenness, composition, and functional diversity of hemlock and mixed hardwood forests, we generated hypotheses for how arthropod diversity in the mid-Atlantic region of the U.S. might respond to HWA-induced hemlock declines and the subsequent expected succession to mixed hardwood forest. Because the mixed hardwood forest had more arthropod individuals and families but similar evenness as the hemlock forest, we hypothesize that the

replacement of hemlock forests with mixed hardwood species will result in an increase in arthropod abundance and alpha diversity without any change in relative abundance (at the family level; see also Ellison et al., 2005b). Identifying taxa that were found predominantly in hemlock or hardwood forests increases our ability to predict which specific arthropod taxa might decline and increase, respectively, in response to the expected hemlock-to-hardwood succession. We hypothesize declines for the seven hemlock indicator taxa and increases for the 23 hardwood indicator taxa that will be proportional to the difference between their permuted (randomized) and observed indicator values. Most of these indicator taxa are abundant and important members of the forest food web, suggesting that changes in their abundance could have substantial direct and indirect effects on these food webs. These taxa habitat associations, as well as the greater taxonomic similarity within the hardwood forest than between the hardwood and hemlock forest, suggest that arthropod beta diversity might decline as HWA-afflicted regions become more homogeneously mixed hardwood (see also Ellison et al., 2005b). However, given that we only studied two forests, this study must be considered exploratory and hypothesis generating rather than hypothesis testing.

Although we predict that seven arthropod taxa will decline with hemlock losses, this is undoubtedly an underestimate for several reasons. First, greater temporal breadth and more intensive sampling would likely add to the list of arthropod hemlock “specialists.” Second, our species-level identification was far from complete due to the lack of available taxonomic specialists that is

crippling biodiversity and conservation research worldwide (Godfray, 2002). Finer taxonomic resolution will likely identify additional hemlock indicator taxa. Finally, it is impossible to have a comprehensive understanding of changes in arthropod diversity or its attendant impacts when so many North American arthropod species remain undescribed, another by-product of the taxonomic impediment (Kim and Byrne, 2006). This was illustrated by the eleven undescribed insect species discovered in this inventory. Although greater species-level identification would be ideal, family level identification might actually be most relevant for management and monitoring purposes because, for most invertebrates, the funds and expertise are not presently available to readily identify individuals below this taxonomic level (exceptions might be at-risk, invasive, or pest species; Rohr et al., 2007).

Despite underestimating losses, this study provides important recommendations for fine-filter monitoring of taxa that might be most threatened by hemlock declines (i.e. the seven hemlock indicator taxa), especially given that the gravity and urgency of foundation species losses often necessitates decisions made on sparse and uncertain data. A defensible fine-filter approach can be more cost-effective than coarse-filter monitoring (Rohr et al., 2007), freeing time and funds for obtaining precious baseline data needed for monitoring and for better understanding important species interactions and community processes. Further, conservation decisions regarding habitat loss should ideally be based on biodiversity that is integral to fundamental ecosystem processes and on a majority of the biodiversity in the impacted system. Arthropods are often vital to ecosystem functions and represent the majority of macroscopic biodiversity in most ecosystems (Kremen et al., 1993). Hence, by indiscriminately enumerating virtually all arthropods (in a season of their peak abundance) and providing hypotheses regarding which might decline and increase, we provide managers a defensible starting point for monitoring. Rarely are information and predictions available for such a large proportion of macroscopic biodiversity.

However, caution should be taken extrapolating our findings beyond the specific forests examined, and sampling additional forests and regions will undoubtedly be necessary to determine the generality of our results. That is why re-sampling portions of the Shenandoah hemlock forest post-hemlock mortality and testing our predictions in other regions are in the planning stages. Nevertheless, there are many promising consistencies between our results and those from other regions that suggest that we may be moving toward identifying general patterns in compositional change that will ensue following HWA infestations. For example, at Shenandoah National Park, Diplopoda and Chilopoda had strong associations with the hemlock forest relative to the sampled hardwood forest (Table 2), a result consistent with that found by Hartman (1977) for hemlock and hardwood stands in Connecticut. Additionally, Snyder et al. (2002) discovered that stoneflies in the family Leuctridae were strongly associated with hemlock stands and Ellison et al. (2005b) showed changes in ant communities in response to hemlock declines, results supported by our indicator analyses for the mid-Atlantic region of the U.S. (Table 2). In addition, substantial changes in vertebrate diversity are also expected with hemlock losses (Tingley et al., 2002; Snyder et al., 2002; Ross et al., 2003). Thus far, the prospect for identifying general compositional changes in response to hemlock declines, at least at broad taxonomic resolution, remains hopeful.

Although our results suggest that the expected succession will cause changes in arthropod community structure, we found no evidence supporting parallel changes in the composition of arthropod functional (feeding) groups, perhaps owing to functional redundancies within the forests. This should not be taken to mean that there will be no changes in ecosystem functions with hemlock losses. On the contrary, research that more thoroughly and more

directly examined the consequences of hemlock losses and changes in tree species composition on ecosystem functions points to substantial changes in biogeochemical processes and nutrient dynamics (Jenkins et al., 1999; Kizlinski et al., 2002; Stadler et al., 2005, 2006).

Like any model, the comparative approach used here has assumptions that can be relaxed and parameters that can be difficult to estimate. For instance, it requires knowing something about the successional dynamics following a foundation species loss. While there are likely to be some general successional responses to foundation species declines, the fact that context dependencies and geographic variation are widespread and can alter temporal dynamics suggests that there is just as likely to be substantial variability surrounding these generalities that cannot be ignored (Strayer et al., 2006). An underlying assumption of the employed comparative framework is that changes in environmental conditions or evolutionary responses will not alter the outcome of succession or the responses of biodiversity to succession. Finally, another challenge is the likelihood that pest and pathogen invasions, succession, and biological responses depend on initial conditions (e.g. Jenkins et al., 2000) and additive or synergistic interactions among biotic and abiotic stressors.

The comparative framework does provide three key contributions to the foundation and invasive species literature that might out-weigh the aforementioned and unmentioned limitations. First, it offers a straightforward approach for obtaining important, initial, coarse- and fine-scale predictions for responses to foundation species declines that can help target early monitoring, management, and conservation efforts. Second, it provides the scaffolding upon which more sophisticated and precise predictive models can be built (e.g. Gotelli and Ellison, 2006). As we learn more about the specific context dependencies, spatiotemporal scales, multiple stressors, and additive and synergistic interactions that influence impact trajectories, they can be added to this scaffolding to improve our predictions. Third, it directly addresses recent entreaties that not only advocate more studies on invasive species, but also a shift in research effort towards forecasting the effects of invasions so that proactive and preventative measures can be implemented in impacted ecosystems (Lawler et al., 2006; Lovett et al., 2006; Strayer et al., 2006). In the absence of a better approach, the comparative methodology used here certainly has merit over doing nothing at all.

Foundation species declines will undoubtedly be a major environmental and economic concern into the future (Ellison et al., 2005a; Lovett et al., 2006). For instance, there are countless present and emerging threats to foundation tree species, such as the gypsy moth, emerald ash borer, Asian long-horned beetle, balsam woolly adelgid, and *Phytophthora ramorum* (the cause of sudden oak death) to name a few, as well as numerous emerging threats to other foundation species, such as the adverse effects of pollution, climate change and disease on corals (Harvell et al., 1999, 2002). Admittedly, our rapidly changing world will require that predictions be based on incomplete information, making it difficult to accurately forecast the impacts of foundation species declines (Lovett et al., 2006). Nevertheless, due to the gravity of foundation species losses, we believe that this uncertainty should not preclude forecasting or taking conservation action. Rather, decisions should be made that weigh the costs of doing nothing versus the costs of making potentially poor management decisions because of inevitable uncertainty. We hope that this study encourages earlier predictions and promotes additional predictive-based research on responses to foundation species declines so that the catastrophic outcomes of our previous late and ineffective responses to foundation species losses are less likely to repeat themselves.

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