wildlife management

Family Richness and Biomass of Understory Invertebrates in Early and Late Successional Habitats of Northern New Hampshire

Matthew K. Wilson, Winsor H. Lowe, and Keith H. Nislow

In the northeastern United States, many vertebrate species rely on early successional forest habitats (ESHs). ESHs may also support higher invertebrate diversity and abundance than late successional habitats (LSHs). We assessed the differences in family-level richness and biomass of understory terrestrial invertebrates during the summer season in paired ESH (3–7 years since harvest) and LSH (>50 years since last harvest) stands in the northern hardwood forests of northern New Hampshire. Invertebrate family richness was 1.5 times greater in ESH, with 35 families found only in ESH compared with 5 families found only in LSH. Invertebrate biomass was 3.2 times greater in ESH than in LSH. Our sampling methodology and time frame were limited, and taxonomic resolution was relatively coarse. Nevertheless, our results suggest that including ESH stands in northeastern managed forest landscapes may help maintain high levels of invertebrate diversity and are consistent with the use of ESH by many insectivorous vertebrates.

Keywords: biodiversity, early successional forest habitat, forest management, New England, terrestrial invertebrates

Habitat heterogeneity is important for supporting plant and animal diversity. In the northeastern United States, early successional habitat (ESH), characterized by abundant short-statured woody vegetation, abundant and diverse herbaceous vegetation, and a high productivity:biomass ratio, results from natural and anthropogenic disturbances and contributes heterogeneity to forested landscapes. ESH in this region is created and maintained by natural disturbance processes (windstorms, ice storms, fires, drought, and insect and disease infestations) (Litvaitis 2003a), but forest management is perhaps the most important single process for these habitats (Lorimer 2001). ESH is critical to many species of vertebrates in northeastern forests, including birds, bats, and small mammals (King and Schlossberg 2014). De-Graaf and Yamasaki (2001) listed 40 New England wildlife species (12% of the re-gional wildlife fauna of 338 species) that are restricted to ESH and only 32 species (10%) as not using ESH in combination with other forest size classes. A common explanation for the frequent use of ESH by vertebrates is higher abundance of invertebrate prey relative to surrounding forests (e.g., Chandler et al. 2012). However, studies evaluating community-level differences in invertebrate richness and biomass in ESH and late successional habitat (LSH) are rare (Loeb and O'Keefe 2011). Furthermore, although the steady decline of ESH in the northeastern United States over recent decades has led to special-status designations of plants and vertebrates that rely on this habitat (DeGraaf and Yamasaki 2001), the implications of decreasing ESH for invertebrate taxa have received little consideration.

Several characteristics of ESH vegetation in northern hardwood forests suggest that invertebrate diversity and biomass should be greater in ESH than in LSH, including higher floral diversity (Elliott et al. 2011), a higher productivity:biomass ratio (Horn

1974), and higher nutrient content and reduced secondary compounds (Ohgushi 1992). This increase in plant diversity, nutrient content, and palatability should benefit invertebrate growth and reproduction and improve invertebrate resistance to parasites and disease. Because of the high floral abundance in ESH and the patchy nature of this habitat across the landscape, we expect that invertebrates that rely on this habitat will be winged and have greater dispersal ability than invertebrates that rely on LSH (Brown 1984). However, to date, most studies comparing invertebrate richness and biomass in ESH and LSH limit sampling to one order or family (for review, see Lewinsohn et al. 2005). We are aware of no study comparing broader, community-level responses of invertebrates to ESH and LSH of the northeastern United States. Furthermore, community-level responses to ESH of invertebrates appear to vary by region, highlighting the importance of collecting region-specific data (Lewinsohn et al. 2005). Understanding broader invertebrate responses to ESH in northeastern forests is especially important, given the declining trajectory of ESH cover in the northeastern United States (Trani et al. 2001).

Our goal was to measure how invertebrate family richness, community composition, biomass, and abundance differ between ESH and LSH understories in the northern hardwood forests of northern New England. To meet this goal, we used colored pan traps to sample invertebrates in ESH and LSH focal patches in 12 small watersheds in northern New Hampshire, USA, during July and August 2010. We defined ESH as clearcut patches ranging from 3 to 7 years old and LSH as intact northern hardwood forest >50 years old. These categories are relative and are based on the predominant range of forest stages in managed landscapes of northern New England, including the study area in northern New Hampshire (Miller et al. 1998, Greenberg et al. 2011a, Swanson et al. 2011). Specifically, it is important to note that we did not define LSH as old-growth northern hardwood forest, which is rare in the study region (Ducey et al. 2013). Using understory trap data, we quantified invertebrate family richness, biomass, and abundance in the two habitat types, as well as dissimilarity in family-level community composition between the two habitats. Finally, to address the potential influence of total watershed coverage of ESH and ESH patch size on invertebrate communities, we tested whether these landscape-level variables were related to invertebrate family richness and biomass in focal ESH patches. By focusing at the family level, we sacrifice resolution of patterns of diversity at finer taxonomic levels (e.g., genus and species). However, family-level data are often used to assess taxonomic diversity for use in management decisions (e.g., Adkins and Rieske 2013, Bennett and Gratton 2013), and recent studies showed that such higher levels of taxonomic resolution are often strongly correlated with species-level patterns (Kallimanis et al. 2012, Timms et al. 2013). Nevertheless, the taxonomic resolution of this study, as well as its temporal and geographic constraints, may limit our scope of inference.

Methods

Study Area and Watershed Characteristics

Study sites were located in 12 first- and second-order watersheds of the Dead Diamond River drainage of New Hampshire, USA. (Figure 1). ESH and LSH focal patches were paired within eight of these watersheds. The four remaining watersheds did not have patches of both ESH and LSH large enough to meet the invertebrate sampling criteria. However, these watersheds had sufficiently large patches of one habitat type (ESH in two watersheds and LSH in two watersheds), so the sampling design remained balanced at the stand level. Watersheds differed in their total percent coverage of ESH and focal patches of ESH differed in size (Table 1). We measured both of these characteristics from aerial photographs in IDRISI (Taiga 2009). All study sites were between 582 and 683 m in elevation (Table 1).

The entire Dead Diamond drainage experienced heavy timber harvest in the late 1800s and early 1900s, and its headwater drainages have experienced various degrees of clearcut and selective harvest since the 1930s (Kevin Evans, Dartmouth College Woodlands Office, pers. comm., Apr. 17, 2010). Within these watersheds, stand ages ranged from 0 to approximately 70 years old. LSH (>50 years old) was composed of mixed conifer and deciduous vegetation with a distinct overstory; ESH (3–7 years old) was composed of shrubs and short-statured deciduous trees. Tree species in the LSH included red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), speckled alder (*Alnus rugosa*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), spruce (*Picea* spp.), and green ash (*Fraxinus pennsylvanica*). ESH was dominated by wild raspberry (*Rubus* spp.) and mapleleaf viburnum (*Viburnum acerifolium*).

Invertebrate Sampling

We sampled invertebrates from ESH and LSH focal patches in the 12 study watersheds in July and August 2010. In watersheds with both patch types, ESH and LSH patches were separated from each other by a minimum distance of 100 m. In each patch, five replicate arrays of three colored pan traps (white, yellow, and blue) were set out at a height of 0.5 m aboveground (Leather 2005). To minimize the influence of edge effects on terrestrial invertebrate samples, all

Management and Policy Implications

Foresters are under increasing pressure to demonstrate, document, and communicate the broader ecological impacts of their actions. Although there is an emerging body of literature on how forest management can protect and improve wildlife habitat and overall biodiversity, critical ecological linkages, taxonomic groups, and regional context are often lacking. In this study, we provide quantitative evidence that in the northern hardwood forests of northern New England, the understories of recently harvested forest stands are associated with higher levels of invertebrate diversity and greater invertebrate abundance and biomass than understories of paired, unharvested stands. Although the sampling methods and sampling time frame were limited, results were consistent with previously observed and well-established characteristics of early successional habitats, including high levels of light and nutrients and high productivity of herbaceous vegetation. The patterns of invertebrate abundance and biomass documented here may explain why early successional habitats are heavily used by a wide range of vertebrate insectivores. Ultimately, we envision that management guides currently including prescriptions for wildlife habitat will also address invertebrate communities and their contribution to forest ecosystem structure and function.
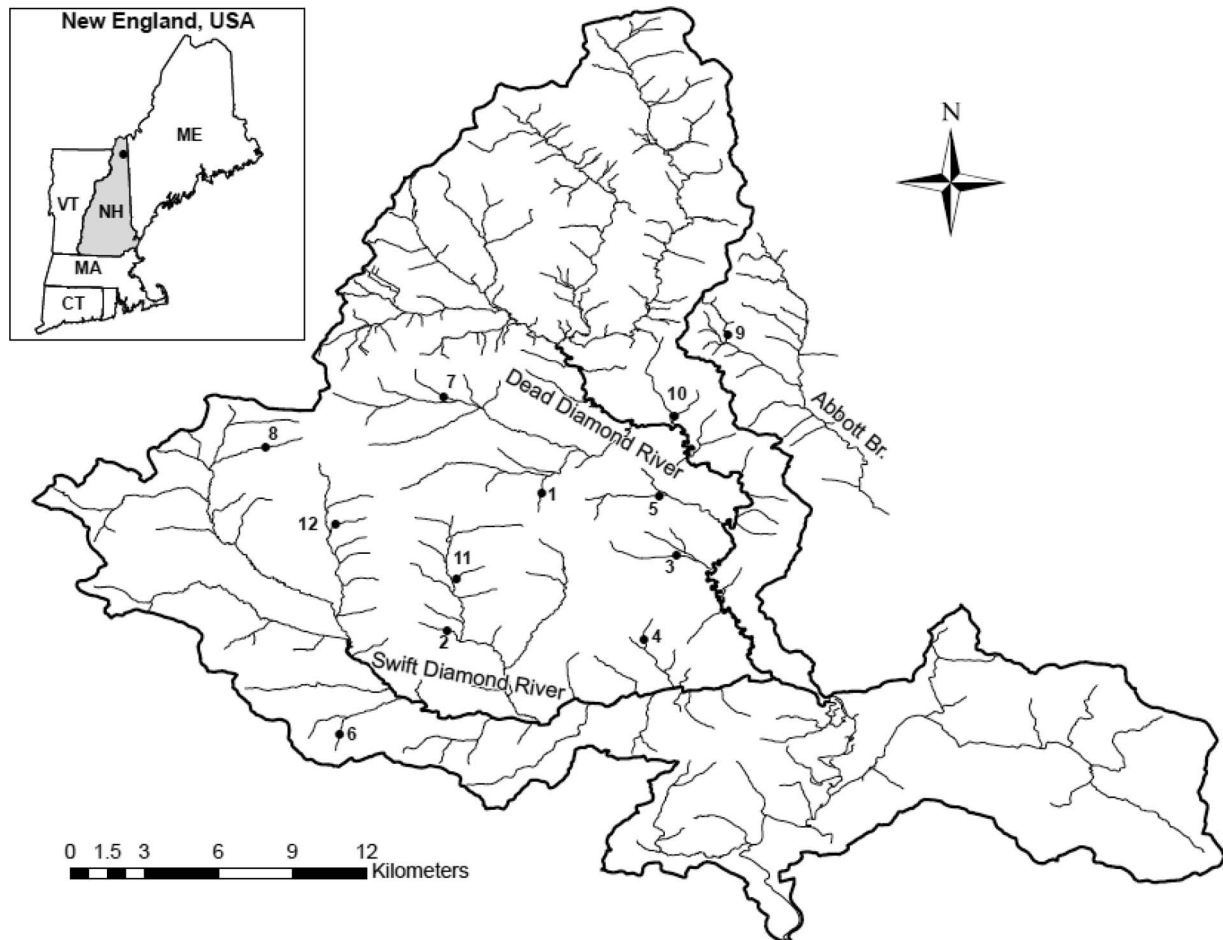
Figure 1. Map of study watershed locations (1–12, corresponding to labels in Table 1) in the Dead Diamond River drainage, New Hampshire, USA.

Table 1. Descriptive characteristics (watershed area, elevation, and % ESH) of the 12 study watersheds and their focal ESH patch size.

Watershed and focal patch characteristics	Watershed											
	1	2	3	4	5	6	7	8	9	10	11	12
Watershed area (ha)	129	130	384	225	403	150	406	348	208	177	105	165
Mean focal patch elevation (m)	742	672	618	677	653	825	812	775	637	582	695	836
% ESH in the watershed	0	1.6	2	2.4	5.7	9.2	11.1	16.8	19.1	24.2	36.7	51.5
Focal ESH patch size (ha)	NA	NA	4.1	4.5	3.9	11.7	5.6	23.1	10.1	5.4	25.7	5

Mean focal patch elevation is the mean of the elevations of ESH and LSH focal patches within the watershed, which differed by no more than 30 m in elevation in all watersheds. Focal ESH patch size and % ESH in the watershed were used to assess their influence on ESH invertebrate richness and biomass. NA, not applicable.

traps were placed at least 30 m from the ESH to LSH transition. Pan trap arrays were randomly placed ~35 m apart inside of focal patches and left open for two 48-hour, rain-free, low-wind periods beginning on July 4 and August 19. Each pan trap was filled with water to a depth of 3 cm and a drop of soap to break the water's surface tension.

For each pan trap array, trapped invertebrates were pooled into a single composite sample and preserved in 70% ethanol. All invertebrates were identified to the family level with the exception of larval invertebrates and spiders (Superorder Araneae),

which were low in abundance (combined, <1% of sampled individuals). Body lengths were measured to the nearest 0.5 mm, and dry masses were calculated with taxon-specific length-mass conversion equations (Sample et al. 1993). This method is recommended for trapped invertebrates because specimens may have lost mass due to partial decomposition while in traps.

We quantified family richness, community composition, biomass, and abundance based on data from the 10 replicate trap arrays (5 arrays per sampling session, 2 sampling sessions) for each of the 10 ESH and

LSH focal patches across the 12 study watersheds. We selected pan traps as a sampling method because they provide low bias while sampling a high diversity of invertebrate taxa, including aerial pollinating, phytophagous, and predatory invertebrates (Leather 2005) and because sample sizes are small enough to allow sufficient replication for statistical analyses. However, no terrestrial invertebrate trap is completely without bias. We cannot exclude the possibility that the visibility of pan traps by invertebrates was greater in open ESH, and several important invertebrate groups are not sampled by this

Table 2. Mean abundance and biomass of invertebrate families, based on data from pan traps in patches of ESH and LSH in 12 watersheds in northern New Hampshire, USA.

Order/family	Mean abundance		Mean biomass (mg)	
	ESH	LSH	ESH	LSH
Aranae				
Araneae—other	1.17	1.35	3.51	3.48
Pholcidae	0.05	0.00	1.59	0.00
Salticidae	0.25	0.00	3.95	0.00
Coleoptera				
Buprestidae	0.40	0.05	8.79	3.56
Cerambycidae	0.45	0.25	11.05	8.93
Chrysomelidae	0.10	0.00	2.39	0.00
Coccinellidae	0.10	0.00	16.71	4.24
Curculionidae	0.65	0.35	3.07	0.00
Dermestidae	0.17	0.05	1.53	0.73
Elateridae	0.20	0.10	10.69	8.02
Eucinetidae	0.05	0.00	0.24	0.00
Glaphyridae	1.12	0.00	58.27	0.00
Lampyridae	0.20	0.00	88.80	0.00
Lycidae	0.05	0.00	5.68	0.00
Melyridae	0.05	0.00	6.44	0.00
Mordellidae	0.66	0.05	7.49	7.62
Mycetophagidae	0.05	0.00	0.32	0.00
Nitidulidae	0.30	0.15	1.23	14.12
Ptiliidae	0.05	0.00	0.05	0.00
Scarabaeidae	0.05	0.05	6.77	24.24
Staphylinidae	1.44	4.79	4.07	4.86
Diptera				
Anthomyiidae	1.90	1.09	10.54	6.15
Asilidae	0.57	0.17	19.94	14.12
Aulacigastridae	0.15	0.05	1.39	0.18
Bombyliidae	0.05	0.00	7.87	0.00
Calliphoridae	0.86	0.00	17.28	0.00
Camillidae	3.87	0.98	3.20	0.75
Cecidomyiidae	2.35	4.08	0.29	0.38
Ceratopogonidae	0.39	0.15	0.16	0.12
Chamaemyiidae	0.05	0.00	0.12	0.00
Chironomidae	6.02	4.96	0.49	0.47
Chloropidae	0.73	0.55	1.00	0.87
Conopidae	0.25	0.10	10.92	4.39
Diptera (larvae)	2.00	0.00	5.58	0.00
Dolichopodidae	5.26	1.84	14.46	5.33
Drosophilidae	0.43	0.15	0.88	0.74
Dryomyzidae	0.10	0.23	2.57	6.67
Empididae	1.72	2.54	7.24	7.60
Heleomyzidae	0.20	0.30	3.59	3.67
Lauxaniidae	0.30	0.30	2.82	3.70
Milichiidae	0.05	0.00	0.21	0.00
Muscidae	6.88	4.62	56.51	30.47
Mycetophilidae	0.76	1.15	3.01	1.77
Phoridae	1.98	3.64	2.34	3.82
Piophilidae	0.05	0.05	1.02	0.67
Pipunculidae	0.28	0.10	2.84	1.07
Platypezidae	0.10	0.05	5.33	11.43
Psychodidae	0.64	0.62	0.55	0.58
Ptychopteridae	0.05	0.00	4.16	0.00
Rhagionidae	0.05	0.00	1.11	0.00
Scatopsidae	6.15	5.09	0.43	0.41
Sciaridae	1.40	2.12	0.73	0.81
Sciomyzidae	0.05	0.05	3.29	6.09
Sepsidae	1.09	0.15	5.65	3.39
Simuliidae	0.86	0.15	0.51	0.39
Sphaeroceridae	0.30	0.38	1.07	0.80
Stratiomyidae	0.15	0.00	17.91	0.00
Syrphidae	3.12	0.79	32.82	9.62
Tabanidae	0.53	0.10	19.43	11.77
Tachinidae	2.25	0.96	24.51	12.33
Tephritidae	0.10	0.00	5.67	0.00
Therevidae	0.13	0.00	25.56	0.00
Tipulidae	1.59	3.03	3.63	6.51

method, including nonflying species, forest floor species, and canopy species. Species in these groups may be important components of overall invertebrate diversity in late successional forests. Therefore, it is crucial to acknowledge that our study targeted a subset of overall invertebrate diversity, but one that we expected to be important in both ESH and LSH (unlike canopy species, for example). Further, we chose to restrict the sampling period to midsummer as it is a season of maximum biological activity in northern New England forests and gave us the best opportunity to obtain insects in stages that were readily identifiable at the family level.

Data Analysis

To assess differences in family richness in ESH and LSH at sampling intensities ranging from 1 to 10 watersheds, we estimated the richness of the family pool from the sample distribution of each habitat type using nonparametric Mao Tau estimators with EstimateS, version 8.2 (Colwell 2011). This resulted in sample-based accumulation curves with 95% confidence intervals (CIs) calculated from 5,000 reshufflings of the sample order. Accumulation curves did not reach an asymptote, so we used the first-order jackknife method in EstimateS to estimate asymptotic family richness in ESH and LSH; this method adjusts for bias due to taxa being missed during sampling. The 95% CIs were calculated from 5,000 reshufflings of sample order.

We used nonmetric multidimensional scaling (NMDS) implemented by an analysis of similarities (Clarke 1993) to display and test for dissimilarities in invertebrate family composition between habitat types using the Jaccard (for the presence or absence of data) and Bray-Curtis (for abundance data) indices of dissimilarity (Venables and Ripley 2002). Two axes of ordination in this NMDS analysis allowed for easy interpretation while maintaining acceptable stress (<15%) and goodness-of-fit values (Kenkel and Orloci 1986). In NMDS, stress is a measure of the mismatch between dissimilarity and ordination values and serves as an alternative measure of goodness of fit.

We used a linear mixed-effects model to test whether the biomass and abundance of understory terrestrial invertebrates differed between ESH and LSH. Habitat type (ESH versus LSH) was modeled as a fixed factor nested within the watershed, which was modeled as a random factor to account for

Table 2. (Continued.)

Order/family	Mean abundance		Mean biomass (mg)	
	ESH	LSH	ESH	LSH
Hemiptera				
Aphididae	1.67	0.72	1.15	0.00
Berytidae	0.10	0.00	0.78	0.00
Cercopidae	0.25	0.05	5.25	3.59
Cicadellidae	2.15	1.69	5.86	0.00
Cicadidae	0.20	0.10	4.76	2.90
Cydnidae	0.98	0.00	19.78	0.00
Membracidae	0.76	0.05	9.38	1.05
Miridae	2.17	0.48	5.70	2.23
Pentatomidae	0.05	0.10	0.05	0.34
Thyreocoridae	0.05	0.00	1.47	0.00
Tingidae	0.00	0.10	0.00	1.09
Hymenoptera				
Aphelinidae	0.15	0.00	0.03	0.65
Apidae	0.42	0.00	58.29	0.00
Braconidae	0.93	1.06	6.06	2.56
Ceraphronidae	1.19	1.10	0.13	0.16
Charipidae	0.10	0.00	0.15	0.00
Crabronidae	0.25	0.00	37.22	1.37
Diapriidae	2.19	6.28	0.41	1.12
Encyrtidae	1.04	0.05	0.18	0.11
Eucoilidae	0.58	0.80	0.12	0.12
Eulophidae	0.45	0.18	0.12	0.22
Eupelmidae	0.90	0.25	0.40	0.68
Figitidae	0.00	0.10	0.00	0.02
Formicidae	0.10	0.15	3.63	1.71
Halictidae	1.92	0.35	19.54	8.05
Ichneumonidae	1.93	3.09	12.39	11.95
Megaspilidae	0.15	0.18	0.25	0.18
Mymaridae	2.48	0.89	0.08	0.02
Mymarommatidae	0.35	0.10	0.06	0.03
Pamphiliidae	1.22	0.65	15.81	10.90
Platygastridae	0.05	0.10	0.05	0.04
Pompilidae	1.10	0.10	16.42	12.48
Pteromalidae	0.05	0.00	0.05	0.00
Scelionidae	0.05	0.10	0.08	0.05
Signiphoridae	0.00	0.05	0.00	0.00
Sphecidae	0.05	0.00	2.93	0.00
Tanaostigmatidae	0.10	0.00	0.02	0.00
Tenthredinidae	0.05	0.00	9.75	0.00
Vespidae	0.84	0.00	31.00	0.00
Lepidoptera				
Coleophoridae	0.15	0.10	1.88	0.48
Hesperiidae	0.53	0.15	128.97	11.69
Lepidoptera (larvae)	0.25	0.53	10.54	11.03
Noctuidae	1.36	1.05	16.67	10.71
Nymphalidae	0.05	0.00	132.48	0.00
Mecoptera				
Panorpodidae	0.43	0.70	60.14	29.95
Orthoptera				
Acrididae	0.35	0.00	66.48	0.00
Romaleidae	0.15	0.00	152.98	0.00
Plecoptera				
Leuctridae	0.05	0.05	2.90	1.75
Nemouridae	0.00	0.15	0.00	1.76
Perlidae	0.00	0.10	0.00	4.56
Caeciliusidae	0.30	0.91	9.41	1.38
Thysanoptera				
Thripidae	1.61	0.93	0.31	0.19

Mean abundance and biomass are for entire ESH and LSH patches and were estimated from five pan trap array replicates in each patch.

variation among watersheds in invertebrate biomass and abundance in both ESH and LSH. A likelihood ratio test was used to assess the contribution of watershed as a random factor (Zuur et al. 2009). We used the same analyses to test whether the abundance of terrestrial invertebrates differed among upland habitat types. Biomass and abundance data used for the analysis were means for each ESH and LSH patch, estimated from the five pan trap arrays. Biomass and abundance data were log transformed for analyses.

Finally, to better understand the differences among watersheds in ESH invertebrate communities, we used linear regression analysis to assess the influence of focal patch size and total percent ESH in the watershed on ESH invertebrate family richness and biomass. Log-transformed, first-order jackknifed estimates of family richness for each focal patch were used in this analysis. These estimates were based on a sampling intensity of 10 replicates within each focal patch. Prior analyses indicated that focal patch size and total percent ESH in the watershed were not correlated (Pearson product moment correlation, $r = 0.30$, $P = 0.39$).

Results

Altogether, 11,347 invertebrates belonging to 11 orders and 115 families were collected in pan traps (Table 2). In addition to spiders (Araneae), 28 families from the insect orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Thysanoptera were present at all sites. Whereas Dipteran families were the most commonly found families in traps, no single order appeared to dominate diversity across sites. True flies in the family Muscidae were the most numerically abundant taxon at ESH sites; wasps of the family Diapriidae were most abundant at LSH sites (Table 2). The grasshopper family Romaleidae had the greatest biomass in ESH sites, and the family Muscidae had the greatest biomass in LSH sites (Table 2).

Family-level richness was significantly greater in ESH than LSH sites. Rarefaction curves estimated 112 families across all ESH sites and 80 families across all LSH sites (Figure 2). Nonoverlapping bootstrapped 95% CI indicate differences in family richness between the two habitat types. The slopes (m) of the curves at a sampling intensity of 10 watersheds ($m = 2.8$ for ESH and $m = 1.5$ for LSH) indicate that the curves did not reach asymptotes and that additional families may be detected with greater sampling intensity. The higher slope of the ESH curve indicates that the gap in family richness between ESH and LSH habitats would increase with sampling intensity. Asymptotic family richness (mean ± bootstrapped 95% CI) was estimated to be 137.2 ± 18.2
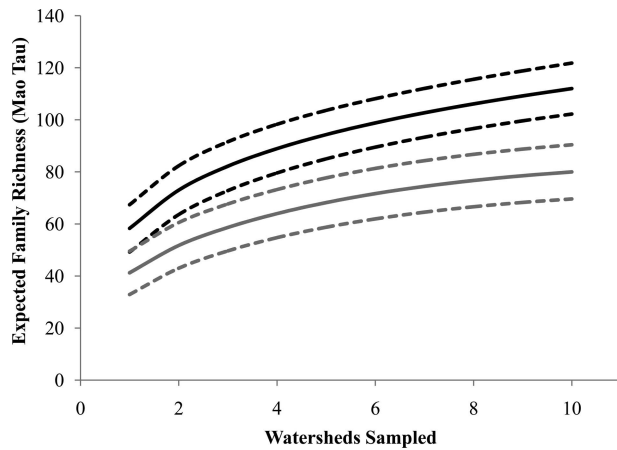
Figure 2. Expected invertebrate family richness (Mao Tau) as a function of number of watersheds sampled, based on data from pan traps in patches of ESH (black line) and LSH (gray line) in 12 watersheds in northern New Hampshire, USA. Dashed lines represent 95% confidence bands.

Figure 3. Predicted asymptotic invertebrate family richness (A), mean dry mass (mg) (B), and abundance (C) of invertebrates based on data from pan traps in patches of ESH and LSH in 12 watersheds in northern New Hampshire, USA. Mean dry mass and abundance are for the entire ESH and LSH patches and were estimated from five pan trap array replicates in each patch. Error bars represent 95% CI. Richness values are first-order jackknife estimates calculated in the program EstimateS.

families for ESH and 93.5 ± 6.7 families for LSH (Figure 3A). Again, nonoverlapping bootstrapped 95% CI indicate differences in family richness between the two habitat types. Regression analysis indicated that family richness was not related to ESH focal patch size ($F_{1,8} = 2.55$, $P = 0.14$) or percent ESH in the watershed ($F_{1,8} = 0.05$, $P = 0.83$).

The results of NMDS with two axes of ordination showed a clear difference in family-level community composition related to habitat type (Figure 4). Dissimilarity in community composition between the two habitat types was statistically significant, based on both occurrence ($r = 0.70$, $P < 0.001$; 100,000 permutations) and abundance ($r = 0.80$, $P < 0.001$, 100,000 permutations). In the NMDS analysis of abundance data, the stress value was 11.81% and the nonmetric R^2 was 0.99. In the NMDS analysis of occurrence data, the stress value was 14.74% and the nonmetric R^2 was 0.98. Whereas 35 families were detected exclusively in ESH, only 5 were detected exclusively in LSH (Table 3).
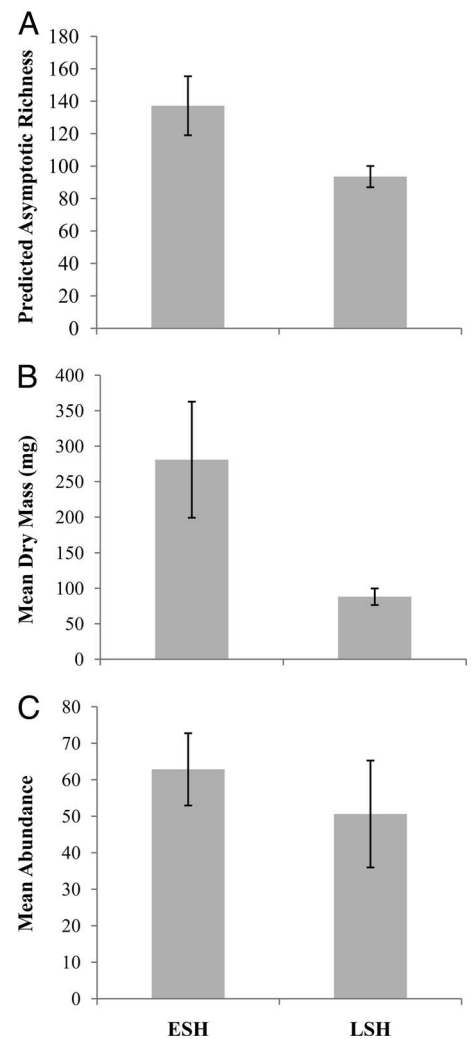
Based on our pan trap samples, invertebrates were more abundant and had higher total biomass in ESH than in LSH sites. Mean invertebrate biomass (±95% CI) was 281 ± 82 mg dry mass in ESH and 88 ± 12 mg dry mass in LSH ($F_{1,8} = 45.94$, $P < 0.0001$) (Table 4; Figure 3B). Mean invertebrate abundance (±95% CI) was 62.9 ± 8 in ESH and 50.6 ± 14 in LSH ($F_{1,8} = 3.65$, $P = 0.057$) (Table 4; Figure 3C). The likelihood ratio test comparing the full mixed-effects model with a general linear model in which the percent ESH in the watershed was excluded (i.e., excluding watershed as a random effect) showed that percent ESH in the watershed had no influence on invertebrate biomass or abundance in focal patches of ESH and LSH ($\chi^2 = 0.0028$, $P = 0.96$, $df = 1$). Biomass was also unrelated to patch size ($F_{1,8} = 0.10$, $P = 0.76$). Percent ESH and patch size values were somewhat skewed toward lower values (Table 1), which may have influenced these results.

Discussion

Our data from pan traps indicate that understories of recently harvested (3–7 years postharvest) ESH patches in northern New Hampshire support a distinct invertebrate community with greater family richness, biomass, and abundance than that of understories of LSH patches that had been unharvested for at least 50 years. General patterns of terrestrial invertebrate response to harvest-induced ESH are probably region-specific (Lewinsohn et al. 2005), and although this study was limited in taxonomic resolution and spatiotemporal scope, ours are the first data on broader, community-level responses for the northern hardwood forests of northern New England. Along with previous studies showing the importance of ESH for a range of taxa in New England and throughout North America (Litvaitis 2001, Howard and Lee 2003, Niemela et al. 2006, Swanson et al. 2011), these data show that including ESH in northeastern managed forest landscapes may contribute to maintaining overall invertebrate biodiversity.

Higher invertebrate biomass and diversity in ESH understory pan traps than in LSH understory pan traps are consistent with a suite of vegetation characteristics associated with ESHs (e.g., high floral abundance, high productivity/biomass ratio, and low levels of defensive compounds). Likewise, regardless of the specific cause, this result is consistent with the strong association of many insectivorous vertebrate species with ESH. For example, Chandler et al. (2012) found that seven of nine mature forest-nesting birds were more abundant in ESH during the postfledgling stage and suggest that this observation is probably due to greater abundance of insect prey. Insectivo-
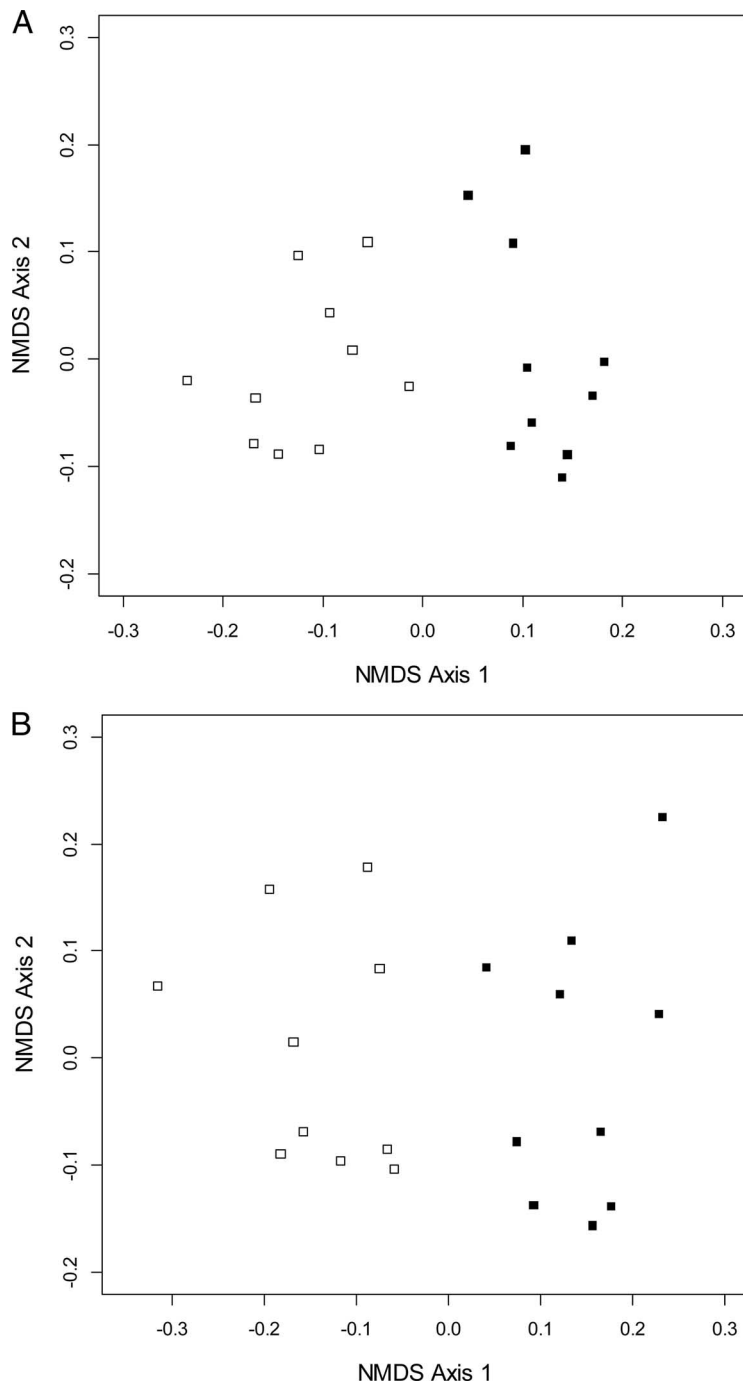
Figure 4. Ordination scores from the NMDS for invertebrate family abundance data (A) and occurrence data (B) from pan traps in patches of ESH and LSH in 12 watersheds in northern New Hampshire, USA. Each point represents the community composition of invertebrates in ESH (□) or LSH (■) patches, where points close in ordination space are compositionally more similar than points that are distant; thus, axes are unitless. Community composition is dissimilar between habitat types.

Table 3. List of families that were detected exclusively in ESH and LSH in pan traps in 12 watersheds in northern New Hampshire, USA.

ESH	LSH
Acrididae	Figitidae
Aphelinidae	Nemouridae
Apidae	Perlidae
Berytidae	Signiphoridae
Bombyliidae	Tingidae
Calliphoridae	
Chamaemyiidae	
Charipidae	
Chrysomelidae	
Coccinellidae	
Crabronidae	
Cydnidae	
Diptera (Larva)	
Eucinetidae	
Glaphyridae	
Lampyridae	
Lycidae	
Melyridae	
Milichiidae	
Mycetophagidae	
Nymphalidae	
Pholcidae	
Pteromalidae	
Ptiliidae	
Ptychopteridae	
Rhagionidae	
Romaleidae	
Salticidae	
Sphecidae	
Stratiomyidae	
Tanaostigmatidae	
Tenthredinidae	
Tephritidae	
Therevidae	
Thyreocoridae	

rous bat foraging activity is also greater in ESH (e.g., Brooks 2009), and the abundance of small, insectivorous mammals often increases with creation of ESH by timber harvest (e.g., Kirkland 1990). Our samples were not restricted to prey of specific vertebrates, and pan traps do not target some important groups of invertebrate prey (e.g.,

canopy and soil invertebrates). Nevertheless, the increased invertebrate biomass and abundance in ESH we observed may be relevant to diverse vertebrate taxa.

Mean family richness in understory pan traps was 1.5 times greater in ESH than in LSH. In addition to the factors mentioned above, this result may be explained by the

greater floral abundance and understory plant diversity found in ESH (Greenberg et al. 2011b). This result is consistent with studies in other regions, but studies have also reported reduced richness of invertebrate groups in ESH (e.g., Summerville and Crist 2002) and no differences in richness of ESH and LSH (e.g., Jeffries et al. 2006). A major part of the variation among studies is probably associated with regional differences in logging practices, forest dynamics, and environmental characteristics. For example, logging in the New England region is generally associated with small-scale selection or group cuts (Miller et al. 1998), as opposed to the extensive even-aged management characteristic of Pacific Northwest forests. Natural regeneration of logged stands is also rapid in New England and leads to increased plant diversity, whereas drier, high-relief, conifer-dominated forests in the western United States experience slower regeneration and moderate changes in plant diver-

Table 4. Mean invertebrate abundance, biomass, and estimated richness (first-order jackknife), based on data from pan traps in patches of ESH and LSH in 12 watersheds in northern New Hampshire, USA.

Site	Abundance ESH	Abundance LSH	Biomass (mg) ESH	Biomass (mg) LSH	Estimated richness ESH	Estimated richness LSH
1	NA	42	NA	94	NA	52
2	NA	37	NA	83	NA	49
3	76	28	483	85	73	44
4	50	33	251	88	76	52
5	65	48	330	130	61	50
6	58	96	143	102	75	59
7	51	43	149	84	68	48
8	66	64	222	72	73	51
9	80	36	389	57	106	53
10	41	NA	133	NA	53	NA
11	75	80	474	86	80	63
12	67	NA	234	NA	57	NA
Mean (±95% CI)	63 (±8)	51 (±14)	281 (±82)	88 (±12)	137 (±18)*	94 (±6)*

Mean abundance and biomass are for entire ESH and LSH patches and were estimated from five pan trap array replicates in each patch. Focal patch-specific richness was estimated from 10 replicate samples (5 from each site in two sampling sessions). NA, not applicable.
* Total asymptotic richness estimates for ESH and LSH are based on 10 replicates of watershed means and SD calculated from bootstrapping. Two watersheds did not have large enough ESH habitat, and two additional watersheds did not have large enough LSH habitat to meet the criteria for invertebrate collection.

sity. Here again, however, it is important to recognize that our study focuses on a subgroup of invertebrates (flying understory species) during July and August, which limits our ability to address the overall patterns of invertebrate diversity in ESH and LSH of the study region.

We found that invertebrate family richness and biomass were unrelated to focal patch size and percent ESH in the study watersheds. This result suggests that even small patches of ESH in an otherwise forested watershed may increase watershed-level invertebrate richness at the family level. However, our minimum ESH patch size (3.9 ha) was relatively large compared with those in studies that have observed correlations between patch size and invertebrate communities (e.g., Shure and Phillips 1991). So, although the lack of relationship between ESH patch size and invertebrate family richness suggests that no additional increase in richness is gained in patch sizes greater than ~4 ha, this study does not address the importance of very small canopy gaps (~0.01 ha) created by natural disturbance or harvest practices such as single tree selection. Furthermore, animal populations are dynamic, particularly invertebrate populations, and the patterns documented here could change significantly throughout the year (Rambo et al. 2014) or among years (Brown 1984); yet we were only able to sample in July and August of a single year. Greater spatial replication across forest types, geographic regions, and forest successional stages of the northeastern

United States. would provide valuable insight on the generality of our findings.

The dissimilarity in family-level community composition between ESH and LSH shows that different understory taxa are reliant on these two habitat types and that including both habitat types on the landscape will benefit regional invertebrate diversity. It is important to keep in mind that this study does not address the patterns of richness at finer taxonomic levels (e.g., genus and species). However, regardless of these patterns, we have documented a clear difference between ESH and LSH in family-level composition of the understory invertebrate community (Figure 4; Table 3) that shows the importance of ESH to regional invertebrate biodiversity. Further research using additional sampling techniques (e.g., pitfall traps, sweep-netting, malaise traps, and blacklight traps) over a broader time frame (including spring and fall seasons over multiple years) is still needed to identify broader patterns of invertebrate response to ESH in this region.

Conclusion

Presettlement coverage of ESH due to natural disturbance in northern hardwood forests was probably low (<5%) (Lorimer and White 2003), and recent estimates indicate that ESH now covers ~17% of northern hardwood forests (Brooks 2003). However, much of the current ESH is in close proximity to human development and heavily affected by associated encroachment of

nonnative plants (Litvaitis 2003b, Johnson et al. 2006). Consequently, a regional decline in ESH coverage could have negative consequences for plants and vertebrates that rely on these habitats if driven by a decline in ESH coverage in undeveloped, managed forest landscapes such as our study area. Our data suggest that including ESH in managed forest landscapes is important for regional invertebrate diversity as well. As forest managers strive to create management plans that allow for ecological and economic benefits (Franklin and Johnson 2012, DellaSala et al. 2013), invertebrate data such as ours become increasingly important for addressing the ecological impacts of management strategies across a broad spectrum of taxa. More data are needed on invertebrate response to the variety of forestry practices used in the northeastern United States and in the variety of forest types of the region. In addition to successional habitats created by commercial clearcut and group selection harvests, proposed management strategies for maintaining native plant–dominated ESH in northeastern forests include encouraging family forest owners to create ESHs (Buffum et al. 2014), maintaining ESHs in powerline rights of way (King et al. 2009), and managing "wildlife openings" by arresting plant succession through repeated mowing or burning (Wagner et al. 2003). Costello et al. (2000) found that songbird species richness was greater in clearcuts of up to 20 ha than in group selection cuts of 0.13–0.65 ha. A similar comparison of invertebrate diversity and biomass in these two types of openings is needed. Although stable, nonsuccessional shrub communities are rare in the northeast, they may also be important for contributing to regional invertebrate diversity.

Literature Cited

ADKINS, J.K., AND L.K. RIESKE. 2013. Loss of a foundation forest species due to an exotic invader impacts terrestrial arthropod communities. *For. Ecol. Manage.* 295:126–135.

BENNETT, A.B., AND C. GRATTON. 2013. Floral diversity increases beneficial arthropod richness and decreases variability in arthropod community composition. *Ecol. Appl.* 23:86–95.

BROOKS, R.T. 2003. Abundance, distribution, trends, and ownership patterns of early-successional forests in the northeastern Unites States. *For. Ecol. Manage.* 185:65–74.

BROOKS, R.T. 2009. Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA. *Biodivers. Conserv.* 18:529–545.

BROWN, V.K. 1984. Secondary succession: Insect-plant relationships. *Bioscience* 34:710–716.

BUFFUM, B., C. MODISETTE, AND S.R. MC-WILLIAMS. 2014. Encouraging family forest owners to create early successional wildlife habitat in southern New England. *PloS One* 9(2).

CHANDLER, C.C., D.I. KING, AND R.B. CHANDLER. 2012. Do mature forest birds prefer early-successional habitat during the post-fledging period? *For. Ecol. Manage.* 264:1–9.

CLARKE, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. *Aust. Ecol.* 18:117–143.

COLWELL, R.K. 2011. *EstimateS: Statistical estimation of species richness and shared species from samples*, version 8.2. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT.

COSTELLO, C.A., M. YAMASAKI, P.J. PERKINS, W.B. LEEK, AND C.D. LEEFUS. 2000. Songbird response to group selection harvests and clearcuts in a New Hampshire northern hardwood forest. *For. Ecol. Manage.* 127:41–54.

DEGRAAF, R.M., AND M. YAMASAKI. 2001. *New England wildlife: Habitat, natural history and distribution.* Univ. Press of New England, Hanover, NH. 496 p.

DELLASALLA, D.A., R.G. ANTHONY, M.L. BOND, E.S. FERNANDEZ, C.A. FRISSELL, C.T. HANSON, AND R. SPIVAK. 2013. Alternative views of a restoration framework for federal forests in the Pacific Northwest. *J. For.* 111:420–429.

DUCEY, M.J., J.S. GUNN, AND A.A. WHITMAN. 2013. Late-successional and old-growth forests in the northeastern United States: Structure, dynamics, and prospects for restoration. *Forests* 4:1055–1086.

ELLIOTT, K.J., C.A. HARPER, AND B. COLLINS. 2011. Herbaceous response to type and severity of disturbance. P. 97–119 in *Sustaining young forest communities: Ecology and management of early successional habitats in the central hardwood region, USA*, Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Springer, New York.

FRANKLIN, J.F., AND K.N. JOHNSON. 2012. A restoration framework for federal forests in the Pacific northwest. *J. For.* 110:429–439.

GREENBERG, C.H., B. COLLINS, F.R. THOMPSON III, AND W.H. MCNAB. 2011a. What are early successional habitats, why are they important, and how can they be sustained? P. 1–10 in *Sustaining young forest communities: Ecology and management of early successional habitats in the central hardwood region, USA*, Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Springer, New York.

GREENBERG, C.H., R.W. PERRY, C.A. HARPER, D.J. LEVEY, AND J.M. MCCORD. 2011b. The role of young, recently disturbed upland hardwood forest as high quality food patches. P. 121–141 in *Sustaining young forest communities: Ecology and management of early successional habitats in the central hardwood region, USA*, Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Springer, New York.

HORN, H.S. 1974. The ecology of secondary succession. *Annu. Rev. Ecol. Syst.* 5:25–37.

HOWARD, L.F., AND T.D. LEE. 2003. Temporal patterns of vascular plant diversity in southeastern New Hampshire forests. *For. Ecol. Manage.* 185:5–20.

JEFFRIES, J.M., R.J. MARQUIS, AND R.E. FORKNER. 2006. Forest age influences oak insect herbivore community structure, richness, and density. *Ecol. Appl.* 16:901–912.

JOHNSON, V.S., J.A. LITVAITIS, T.D. LEE, AND S.D. FREY. 2006. The role of spatial and temporal scale in colonization and spread of invasive shrubs in early successional habitats. *For. Ecol. Manage.* 228:124–134.

KALLIMANIS, A.S., A.D. MAZARIS, D. TSAKANIKAS, P. DIMOPOULOS, J.D. PANTIS, AND S.P. SGARDELIS. 2012. Efficient biodiversity monitoring: Which taxonomic level to study? *Ecol. Ind.* 15:100–104.

KENKEL, N.C., AND L. ORLOCI. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: Some new results. *Ecology* 67:919–928.

KING, D.I., R.B. CHANDLER, J.M. COLLINS, W.R. PETERSON, AND T.E. LAUTZENHEISER. 2009. Effects of width, edge, and habitat on the abundance and nesting success of scrub-shrub birds in powerline corridors. *Biol. Conserv.* 142:2672–2680.

KING, D.I., AND S. SCHLOSSBERG. 2014. Synthesis of the conservation value of the early-successional stage in forests of eastern North America. *For. Ecol. Manage.* In press.

KIRKLAND, G.L. JR. 1990. Patterns of small mammal community change after clearcutting in temperate North American forests. *Oikos* 59: 313–320.

LEATHER, S.R. (ED.). 2005. *Insect sampling in forest ecosystems.* Wiley-Blackwell, Malden, MA. 320 p.

LITVAITIS, J.A. 2001. Importance of early successional habitats to mammals in eastern forests. *Wildl. Soc. Bull.* 29:466–473.

LITVAITIS, J.A. 2003a. Shrublands and early-successional forests: Critical habitats dependent on disturbance in the northeastern United States. *For. Ecol. Manage.* 185:1–4.

LITVAITIS, J.A. 2003b. Are pre-Columbian conditions relevant baselines for managed forests in the northeastern United States? *For. Ecol. Manage.* 185:113–126.

LEWINSOHN, T.M., V. NOVOTNY, AND Y. BASSET. 2005. Insects on plants: Diversity of herbivore assemblages revisited. *Annu. Rev. Ecol. Syst.* 36: 597–620.

LOEB, S.C., AND J.M. O'KEEFE. 2011. Bats and gaps: The role of early successional patches in the roosting and foraging ecology of bats. P. 167–189 in *Sustaining young forest communities: Ecology and management of early successional habitats in the central hardwood region, USA*, Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Springer, New York.

LORIMER, C.G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. *Wildl. Soc. Bull.* 29:425–439.

LORIMER, C.G., AND A.S. WHITE. 2003. Scale and frequency of natural disturbances in the northeastern US: Implications for early successional forest habitats and regional age distributions. *For. Ecol. Manage.* 185:41–64.

MILLER, A.B., E.S. BRYANT, AND R.W. BIRNIE. 1998. An analysis of land cover changes in the northern forest of New England using multi-temporal Landsat MSS data. *Int. J. Remote Sens.* 19:245–265.

NIEMELA, J., Y. HAILA, AND P. PUNTTILA. 2006. The importance of small-scale heterogeneity in boreal forests: Variation in diversity in forest-floor invertebrates across the successional gradient. *Ecography* 19:352–368.

OHGUSHI, T. 1992. Resource limitation on insect herbivore populations. P. 199–241 in *Effects of resource distribution on animal-plant interactions*, Hunter, M.D., T. Ohgushi, and P.W. Price (eds.). Academic Press, San Diego, CA.

RAMBO, T., T. SCHOWALTER, AND M. NORTH. 2014. Canopy arthropod responses to thinning and burning treatments in old-growth mixed-conifer forest in the Sierra Nevada, California. *For. Ecol. Manage.* 326:91–100.

SAMPLE, B.E., R.J. COOPER, R.D. GREER, AND R.C. WHITMORE. 1993. Estimation of insect biomass by length and width. *Am. Midl. Nat.* 129:234–240.

SHURE, D.J., AND D.J. PHILLIPS. 1991. Patch size of forest openings and arthropod populations. *Oecologia* 86:325–334.

SUMMERVILLE, K.S., AND T.O. CRIST. 2002. Effects of timber harvest on forest Lepidoptera: Community, guild, and species responses. *Ecol. Appl.* 12:820–835.

SWANSON, M.E., J.F. FRANKLIN, R.L. BESCHTA, C.M. CRISAFULLI, D.A. DELLASALA, R.L. HUTTO, D.B. LINDENMAYER, AND F.J. SWANSON. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Front. Ecol. Environ.* 9:117–125.

TIMMS, L.L., J.J. BOWDEN, K.S. SUMMERVILLE, AND C.M. BUDDLE. 2013. Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. *Insect Conserv. Divers.* 6:453–462.

TRANI, M.K., R.T. BROOKS, T.L. SCHMIDT, V.A. RUDIS, AND C.M. GABBARD. 2001. Patterns and trends of early-successional forests in the eastern United States. *Wildl. Soc. Bull.* 29:413–424.

VENABLES, W.N., AND B.D. RIPLEY. 2002. *Modern applied statistics with S.* Springer-Verlag, Berlin, Germany. 497 p.

WAGNER, D.L., M.W. NELSON, AND D.F. SCHWEITZER. 2003. Shrubland Lepidoptera of southern New England and southeastern New York: Ecology, conservation, and management. *For. Ecol. Manage.* 185:95–112.

ZUUR, A.F., E.N. IENO, N.J. WALKER, A.A. SAVELIEV, AND G.M. SMITH. 2009. *Mixed effects models and extensions in ecology with R.* Springer, New York. 574 p.