ORIGINAL PAPER

The impact of beech thickets on biodiversity

Jonathan A. Cale · Stacy A. McNulty ·
Stephen A. Teale · John D. Castello

Abstract Beech bark disease has dramatically altered hardwood forest structure and composition across northeastern North America. Extensive overstory mortality has resulted in prolific root-sprouting in some stands leading to the development of understory thickets of clonal small-stemmed beech. Beech thickets may impact local forest biodiversity, but this has not been adequately evaluated. We hypothesized significant differences in diversity of groundcover flora, craneflies, amphibians, and small mammals between plots with and without beech thickets. Paired plots were established in uneven-aged northern hardwood forest stands with no recent management history at two sites in the Adirondack Mountains of New York State. Groundcover plants, terrestrial craneflies, amphibians and small mammals were sampled on twenty paired plots. Discriminant analysis showed a significant difference between thicket and non-thicket (control) areas; significant variables in plot type separation were beech sapling abundance, leaf litter depth, and coarse woody debris volume. Groundcover plant cover, richness, and diversity were significantly lower in thicket compared to non-thicket plots, while beech sapling density explained 17–38 % in groundcover plant species diversity. There were no significant differences between the diversity of cranefly, amphibian and small mammal communities of each plot type. Beech thickets are important determinants of local biodiversity.

Keywords Beech bark disease · *Neonectria* · *Cryptococcus fagisuga* · Forest structure

J. A. Cale (✉) · S. A. Teale · J. D. Castello
Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA
e-mail: jacale@syr.edu

S. A. Teale
e-mail: sateale@esf.edu

J. D. Castello
e-mail: jdcastello@esf.edu

S. A. McNulty
Adirondack Ecological Center, State University of New York College of Environmental Science and Forestry, Newcomb, NY 12852, USA
e-mail: smcnulty@esf.edu

Introduction

Biodiversity is associated with many ecosystem functions and services including productivity, stability, and nutrient availability (Tilman 1999). Species diversity in an ecosystem often depends on the foundation species such as dominant tree species that define and influence the ecosystem; consequently, factors affecting foundation species indirectly affect local abiotic conditions, other forest species, and

ultimately biodiversity (Ellison et al. 2005). Invasive forest insect pests and pathogens influence ecosystem functions and the forest biota by altering resource availability (Loo 2009; Lovett et al. 2006).

In the Northern Hardwood Forest (NHF) of northeastern North America, American beech (*Fagus grandifolia* Ehrh.) is a dominant canopy species that fits the definition of foundation species in several ways. It is a major component of three NHF cover types (Eyre 1980), is long-lived, and, as the sole source of hard mast in the NHF, disproportionately influences wildlife populations (Jakubas et al. 2005). Wounding of American beech roots induces adventitious bud formation, from which clonal root sprouts develop (Jones and Raynal 1988). This species is severely affected by beech bark disease (BBD) in much of its geographic range (Morin et al. 2007). The BBD complex involves the invasive beech scale (*Cryptococcus fagisuga* Lind.) and one or more fungal pathogens of the genus *Neonectria* (Ehrlich 1934; Houston 1994a, b). *Cryptococcus fagisuga* is a hemipteran introduced into North America from Europe around 1890 on European beech (*Fagus sylvatica* L.) trees planted in the botanical gardens in Halifax, Nova Scotia, Canada (Hewitt 1914). Although damage caused by the feeding of this insect is believed to be negligible, infection of phloem and cambial tissue by *Neonectria* (*N. ditissima* and *N. faginata* in the Northeast) significantly damages and often kills host trees after several years of sustained infection (Houston 1994a). In eastern North America, BBD has impacted much of the beech's natural range, significantly altering the structure of forests experiencing extensive mortality of overstory beech (Garnas et al. 2011; Morin et al. 2007; Shigo 1972). Moreover, similar to the response of beech roots to wounding (Jones and Raynal 1988), evidence suggests that mortality induced by BBD triggers a root-sprouting response (Garnas et al. 2011; Houston 1975) similar to the response of beech roots to wounding. Beech bark disease has, therefore, effectively shifted the dominance of beech from the overstory to the understory, where it occurs in dense thickets (Garnas et al. 2011; Shigo 1972).

Despite the long tenure and widespread occurrence of BBD, the effect of beech thickets on the species diversity of NHF communities remains largely uninvestigated. However, beech thickets have been shown to significantly inhibit the regeneration of overstory associates, particularly sugar maple (*Acer saccharum* Marsh.), in northeastern forests (Hane 2003; Nyland et al. 2006). Presumably, this is due to heavy shading of the forest floor beneath the thicket, but also may be related to the phytotoxic effect of leachate from beech litter (Hane et al. 2003).

If beech thickets alter the biodiversity of the NHF, the potential impacts on the plant and animal communities may be profound. For example, by heavily shading the forest floor, beech thickets may significantly reduce the survivorship of developing groundcover plants by restricting access to ambient diffuse light and sunflecks (Chazdon and Pearcy 1991; Dale and Causton 1992; Iason and Hester 1993; Pearcy and Pfitsch 1991). Beech litter is more persistent than that of its associates because of its high lignin content (Melillo et al. 1982). Leaf litter in beech thickets may create a dense litter layer capable of inhibiting emergence of developing seedlings and forest herbs (Sydes and Grime 1981). These factors could potentially restrict the local floral community to only shade-tolerant species capable of emerging through a deep litter layer.

Faunal communities also may respond to the presence of beech thickets. Entomofauna, particularly detritivorous insects such as craneflies (Tipulidae; Diptera), respond to changes in forest structure (Dajoz 2000; Pritchard 1983). Thus, changes in litter quality and coarse woody debris (CWD) availability linked to the development of beech thickets may reduce the diversity of detritivorous insects. On the other hand, thickets may provide a favorably moist environment for forest amphibians by providing them with a contiguous understory canopy, deep litter, and CWD (Gibbs 1998; McKenny et al. 2006; Semlitsch 2002). These characteristics also may favor high small mammal diversity by providing cover and reduced risk of predation (Healy and Brooks 1988; Kirkland 1990).

The objective of this study was to examine how, through the formation of thickets, the invasive BBD complex indirectly impacts biodiversity in the NHF. We investigated the following four hypotheses: (1) groundcover plant and (2) cranefly diversity will be significantly lower in thicket areas; while (3) amphibian and (4) small mammal diversity will be significantly greater in thicket areas. We further postulated that beech sapling density will explain a significant portion of the diversity variance of these communities.

Methods

Site selection and plot establishment

Study sites were selected from NHF (maple-beech-birch) stands of the State University of New York College of Environmental Science and Forestry (SUNY ESF) Huntington Wildlife Forest (HWF; Latitude 43° 57′ 36″ N, Longitude 74° 13′ 12″ W) in Newcomb, NY (Essex and Hamilton Counties) and the SUNY ESF Cranberry Lake Biological Station (CLBS; Latitude 44° 09′ 20″ N, Longitude 74° 47′ 49″ W) in Cranberry Lake, NY (St. Lawrence County). The HWF covers 6,000 ha, has a mean annual precipitation of 1,010 mm, and is located at an elevation of 490–608 m. Major soil types in this forest are of the Becket-Mundell series sandy-loams. The CLBS covers 395 ha, has a mean annual precipitation of 914 mm, and is located at an elevation of 471–498 m. Major soil types are of the Tunbridge-Lyman and Crary-Potsdam complexes with textures ranging from silty-loam to sandy-loam. Selected stands were uneven-aged with a history of only single-tree selection management, but had not been managed for at least twenty-five years. Additionally, these stands had no history of herbicide treatments.

Forty paired plots (n = 20) were established in May 2009: 36 (n = 18) at the HWF and 4 (n = 2) at the CLBS. Two to four plots were established in each of 16 stands (14 at the HWF and 2 at the CLBS). Additionally, plots were categorized into two types defined by the density of understory beech saplings. This density was assessed along a 16 × 2 m belt transect centered on each potential plot. Moving south to north, all trees <5 cm dbh and ≥1.4 m tall were counted. Areas containing ≤16 beech stems (0.5 stems/m²) were classified as non-thickets and those with ≥32 beech stems (1 stem/m²), as thickets. These values were somewhat arbitrary, but corresponded to two visually distinct understory structures. Each plot pair consisted of one of each plot type, i.e., thicket and non-thicket. Plot centers were marked with a PVC pipe driven into the ground. Each plot pair was 150–650 m from any other pair. A distance of 50–60 m separated each plot of a given pair. Slope and aspect measurements were recorded for each plot using a clinometer and compass, respectively. Soil texture (percentage of sand, silt, and clay) and pH were determined for each plot using preexisting spatial datasets (Somers 1986) of soil series distributions at each site.

Vegetation sampling

Forest strata were sampled using circular plots centered on the fixed points. Forest overstory was sampled in 0.04 ha plots (r = 11.5 m). Species and diameter were recorded for all trees ≥5 cm dbh within the plot. These data were used to characterize overstory structure and composition. The understory was sampled using 8 m radial (0.02 ha) plots. All trees <5 cm dbh and ≥1.4 m tall (saplings) were identified to species and counted. Groundcover plants were sampled using five 1 m² nested quadrats within the belt transect. All quadrats were 1 m apart, while those farthest from the plot centers were 1.5 m from the transect ends. The percent cover of all plants less than 1.4 m tall was estimated visually using 5 % cover-classes for each species present. These included bryophytes, graminoids, forbs, ferns, shrubs, and arborescents. Sampling began after most spring ephemeral species had died, however any observed ephemerals were not recorded. Mean cover estimates were averaged across quadrats to obtain the estimated proportion of each species in a plot. Bryophyte and graminoid cover was combined due to low incidence. Additionally, the thickness of the litter layer in each quadrat was estimated by measuring the depth to the Oa horizon in each corner and center. These measurements were averaged for a given quadrat then averaged across quadrats to estimate litter depth for the plot.

Cranefly sampling

Pyramidal emergence traps constructed of white nylon mesh covering four 1 m wooden stakes, were used to collect adult craneflies as they emerged from the soil. Trap bases were open, placed flush against the ground, and covered approximately 1 m² that was free of woody debris. A collection container with a removable lid and killing agent was supported at the trap's apex. Traps were checked every 7 days from May through August 2010. Species determinations were made using the taxonomic descriptions of Crampton et al. (1942).

Amphibian sampling

A twenty minute timed search was conducted simultaneously by three people (60 min/plot) within the 8 m fixed-radius understory plot. All cover objects

(e.g. woody debris and rocks) were turned over, tree bases examined, and litter disturbed in searching for amphibians. Each amphibian was identified to species and released (Amphibian Project # 28 protocol approved 16 February 2010). Plots were sampled once over a two-week period in early June 2010. Each plot pair was sampled on the same day to minimize the influence of weather conditions.

Litter samples were collected and CWD measurements recorded after each timed search. The length and diameter at each end for all woody debris over 5 cm at its smallest end was recorded and used to calculate CWD volume (McGee 2000). Leaf litter was collected from a 0.5 × 0.5 m area 4 m from the plot center in each of the four cardinal directions. These litter samples were pooled, sorted as beech or non-beech, weighed, and used to calculate the beech litter component of each plot.

Small mammal sampling

A 5 × 5 point trapping grid centered over each plot was used to sample small mammals for three consecutive nights from June through August 2010. Grid points were 10 m apart and alternated between having a 7.6 × 7.6 × 25.4 cm folding Sherman trap (H. B. Sherman Traps Inc., Tallahassee, FL, USA) or a 12.7 × 12.7 × 40.6 cm Tomahawk trap (Tomahawk Live-trap Co., Tomahawk, WI, USA). Traps (n = 25) were covered with leaf litter and abutted cover-objects when these were in close proximity to the grid point. Traps were baited each evening and checked the following morning. All captures were recorded by species, marked with non-toxic, non-permanent black ink, and released (IACUC protocol #2010-01). To avoid overestimating species abundance, recaptures were not recorded. Each plot in a pair was sampled simultaneously.

Diversity calculations and statistical analysis

The species diversity of each floral and faunal group was calculated using the Shannon-Wiener and inverse Simpson's indices and richness (Magurran 2004). Stand diameter diversity was calculated using the Shannon-Wiener index (Buongiorno 2001). Descriptive statistics for each community and all subsequent analyses were conducted using SAS 9.2 (SAS Institute 2008). Because it uses pooled within-class variance,

canonical discriminant analysis (PROC CANDISC) was chosen to investigate the separation of plot types in multidimensional space. Fourteen plot characteristics comprised this analysis: beech sapling density, litter depth (cm), aspect (azimuth), slope (degrees), stand diameter diversity, total living basal area (m^2/ha), total dead beech basal area (m^2/ha), soil texture (percentage of sand, silt, and clay), soil pH, CWD volume (m^3), proportion of beech litter, and the number of years since the last stand management. Paired t tests (PROC TTEST) were used to compare mean percent cover of floral functional groups as well as floral community diversity and species richness between plot types. Ordinary least squares regression (OLS; PROC REG) was used to examine the relationship between beech thicket density and groundcover plant diversity, while a Mann–Whitney U-test (PROC NPAR1WAY) was used to test for differences in the diversity of faunal communities between plot types.

Results

Discriminant analysis

Because we had two groups (plot types) a single canonical root was extracted from the discriminant analysis, indicating that non-thickets and thickets were significantly different (Wilk's lambda: 0.0847; $F(13,22) = 18.27$; $p < 0.001$; Fig. 1). Beech sapling density, litter depth, and CWD volume were significant ($p < 0.05$) factors in plot type separation. Several
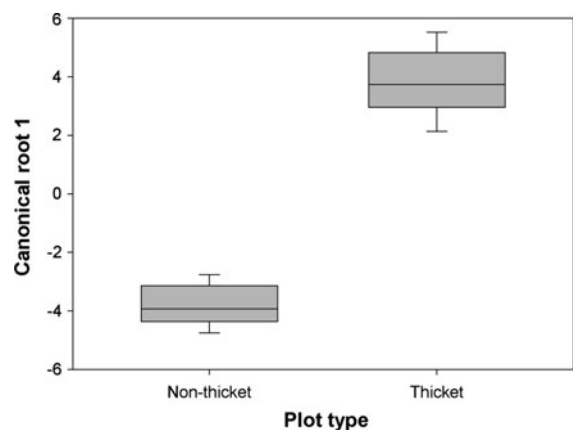

Fig. 1 Boxplot of the canonical roots for each plot type. *Solid boxed lines* and *whiskers* indicate median root and maximum and minimum values, respectively

Table 1 Mean percent cover and diversity (±standard error) and paired *t* test results ($\alpha = 0.05$, df = 19, n = 20) by plot type for groundcover flora

	Mean ± standard		*t*	*p* value
	Non-thicket	Thicket		
All species	33.68 ± 2.54	22.12 ± 1.81	4.96	<0.001
Bryophytes and graminoids	3.68 ± 0.56	2.86 ± 0.66	1.27	0.219
Forbs	2.61 ± 0 45	1.38 ± 0.27	2.57	0.019
Ferns	12.39 ± 1.70	6.01 ± 0.90	4.37	<0.001
Shrubs	6.46 ± 1.43	1.63 ± 0.64	3.39	0.003
Arborescent	8.51 ± 1.47	10.23 ± 1.36	1.99	0.245
Arborescent excluding beech	3.97 ± 0.97	1.8 ± 0.60	3.01	0.007
Shannon-Wiener index (H')	1.66 ± 0.06	1.35 ± 0.07	3.38	0.003
Inverse Simpson's index (1/D)	3.97 ± 0.29	3.13 ± 0.22	2.41	0.027
Species richness	9.95 ± 0.56	6.80 ± 0.43	4.73	<0.001

Table 2 Ordinary least squares regression (df = 38, n = 40) results for each diversity metric against beech sapling density

Variable	Coefficient + standard error	*t*	r^2	*p* value
Shannon-Wiener index (H')	−0.75 ± 0.18	4.10	0.31	<0.001
Inverse Simpson's index (1/D)	−2.04 ± 0.65	2.78	0.17	0.008
Species richness	−6.92 ± 1.27	4.87	0.38	0.001

significant ($p < 0.05$) positive correlations were detected between: beech sapling density and live beech basal area, litter depth and proportion of beech litter, dead beech basal area and CWD, and CWD and proportion of beech litter.

Floral communities

Forty-three groundcover plant species were recorded. A complete species list is provided in Online Resource 1. Plants were observed in all quadrats, and no species covered less than one percent of the area of any single quadrat. Mean beech sapling density was 0.12 (±0.01 SE) stems/m^2 and 0.55 (±0.03 SE) stems/m^2 for non-thicket and thicket plots, respectively. These values were significantly different using a paired *t* test ($t(19) = -12.80$, $p < 0.001$). Mean litter depth for non-thicket and thicket plots was 1.48 (±0.06 SE) and 2.25 (±0.10 SE) cm, respectively, and were significantly different ($t(19) = -7.40$, $p < 0.001$). Additionally, OLS regression indicates litter depth was significantly positively correlated (b = 1.4, $t(38) = 11.7$, $p < 0.001$) with beech sapling density, which explained 33 % ($r^2 = 0.33$, $F(1,38) = 18.7$) of the variance in litter depth. Mean percent cover for vegetational functional groups are shown in Table 1.

Mean cover was significantly ($p < 0.05$) lower in thicket plots for all species combined and all functional groups except bryophytes and graminoids and arborescent vegetation (with beech cover) (Table 1). Because beech primarily of root sprout origin (unpublished data) accounted for 53 and 83 % of all arborescent cover in non-thicket and thicket plots, respectively, beech was excluded from this functional group and the comparison was repeated. Non-beech arborescent cover was significantly lower in thicket plots (Table 1). Mean Shannon-Wiener and inverse Simpson's indices of diversity and species richness were 19, 21, and 32 % lower in thicket plots than non-thicket plots, respectively (Table 1). Beech sapling density was significantly ($p < 0.05$) correlated with all diversity metrics and explained 17–38 % of the variance (Table 2). Because this was an observational study, these regression results cannot be used to interpret cause-and-effect.

Faunal communities

Eighty-one crane flies representing 22 species were collected. No craneflies were captured from 10 plots, and only a single species was collected from 17 plots. Eleven species of amphibians (n = 182) were

recorded during timed searches. No individuals were recorded in four plots, and in 11 plots only a single species was recorded. Seven species of small mammals (n = 271) were captured during 108 trap nights. Captures were recorded from each plot. However, at three plots only a single species was recorded. Total catch per unit effort values are available in Online Resource 2. No significant differences in diversity were detected between plot types for any of the faunal communities examined. A complete species list is provided in Online Resource 1.

Discussion

Thickets of small-stemmed American beech clones arising from the root systems of dead overstory trees affect the diversity of hardwood forest stands in the central Adirondacks. The floral species diversity of this community is significantly lower in thicket areas, which appears to be due to a reduction in cover of most functional groups as well as overall species richness (Table 1). Furthermore, beech sapling density is significantly correlated with floral diversity, explaining 17–38 % of the variance (Table 2). Although this study was observational and not designed to identify mechanisms by which beech thickets impact local diversity, a likely explanation for this relationship is that thickets heavily shade the forest floor, reducing the survivorship of local vegetation. Although many forest plants have developed acclimation strategies to a diffuse-light environment (Rothstein and Zak 2001), excessive and prolonged shading can result in altered nutrient allocation, growth rates, and sexual reproduction (Dale and Causton 1992; Iason and Hester 1993). Additionally, sunfleck utilization accounts for a significant portion of carbon gain allocated to herbaceous biomass and, in the absence of this irradiance, these plants may experience reduced growth, reproduction, and survival (Chazdon and Pearcy 1991; Pearcy and Pfitsch 1991). Hane (2003) showed lower survivorship of sugar maple seedlings in shade cloth treatments when compared to controls. However, survivorship was further reduced when seedlings were grown under a dense beech understory, suggesting that shading is likely not the sole mechanism by which thickets impact local vegetation. Hane et al. (2003) suggested phytotoxic beech litter leachate may act synergistically with shading to reduce the survivorship

of sugar maple seedlings. Sugar maple cover and incidence was significantly lower in thicket plots relative to non-thicket plots (data not shown).

Another possible mechanism by which beech thickets may negatively impact groundcover plant communities is by high local input of leaf litter. Beech litter is highly lignified and decomposes much more slowly than that of its common associates, e.g. sugar maple, red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and paper birch (*Betula papyrifera* Marsh.) (Melillo et al. 1982). This litter is, long-lasting and may contribute to the development of a deep, persistent litter layer over time. Litter persistence is a major determinant of the spatial pattern, species composition and regeneration of forest herbs (Sydes and Grime 1981). Beech litter may inhibit regeneration by preventing the emergence of seedlings and forest herbs.

Forest insects respond to changes in forest structure and composition (Dajoz 2000), which is especially true for detritivorous insects such as craneflies. Craneflies live in the organic horizons of forest soils and their diet is directly linked to woody debris and leaf litter quality and input (Pritchard 1983). Although some cranefly species are known to discriminate against persistent and low quality (low nitrogen, high lignin) leaf litter (Cummins and Klug 1979), we found no evidence to suggest that beech-dominated litter or thicket presence influences cranefly diversity. Our data, therefore, do not support our hypothesis that cranefly diversity is lower in thicket plots.

Forest amphibian diversity is closely tied to the degree of canopy closure, microclimate moisture regime, CWD, and leaf litter depth due to their moisture-dependent life history characteristics (Semlitsch 2002). These animals generally prefer areas with a stable moisture environment, i.e., with ample CWD and closed canopies (Gibbs 1998; McKenny et al. 2006). However, we found no difference in amphibian species diversity between plot types; therefore our data do not support our hypothesis that amphibian diversity will be significantly greater in thicket plots. A possible explanation for this result is that the moisture environment within beech thickets is not significantly different than that in adjacent nonthicket areas. Indeed, Brooks and Kyker-Snowman (2008) showed that the relative humidity in areas of dense regrowth following selection cuttings did not significantly differ from optimal forest amphibian habitat in

paired control sites. Beech thickets may not provide a more beneficial microclimate to amphibians occupying these areas; a focused study of soil moisture and forest floor invertebrate prey may shed more light on the relationship between terrestrial amphibians and beech thickets.

Small mammals within the forest community respond to changes in forest structure (Storer et al. 2005). Forest-dwelling small mammals avoid clearings, preferring instead to occupy densely vegetated areas (Kirkland 1990) with sufficient CWD that afford protection from predation (Healy and Brooks 1988; Kirkland 1990). Abundance of small mammals increases as total understory and ground-layer (shrubs, non-woody, and seedling) cover and richness increases (Muzika et al. 2004). However we found no differences in small mammal diversity between plot types; our data, therefore, do not support our hypothesis that small mammal diversity is greater in beech thickets. We see two possible explanations of these results. Muzika et al. (2004) suggested that increased complexity of these forest strata increase both food supplies and foraging and escape cover for small mammals. The reduced complexity of the vegetation community in beech thickets may not provide small mammals with such benefits; however, our dataset may be too limited to detect differences in the small mammal community in this regard. Additionally, home ranges of some species (*Myodes gapperi, Napaeozapus insignis,* and *Tamiasciurus hudsonsicus* exceed the distance between paired plots (i.e. 50–60 m) (Saunders 1988), suggesting our study design did not capture these animals adequately.

This study highlights how the cascading effects of an invasive disease complex can negatively affect the diversity of non-host species. Beech bark disease has caused extensive mortality of mature beech in stands across eastern North America. In many regions, beech has become the dominant understory species, forming dense thickets which, as shown here, reduce the cover and diversity of groundcover plants. While the relationship of beech thicket formation to faunal communities is less clear, experimental manipulations may shed more light on these dynamics.

References

Brooks RT, Kyker-Snowman TD (2008) Forest floor temperature and relative humidity following timber harvesting in southern New England, USA. For Ecol Manag 254:65–73

Buongiorno J (2001) Quantifying the implications of transformation from even to uneven-aged forest stands. For Ecol Manag 151:121–132

Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants. Bioscience 41:760–766

Crampton GC, Curran CH, Alexander CP (1942) Guide to the insects of connecticut: part VI. The diptera or true flies of connecticut, first fascicle, external morphology; key to families; Tanyderidae, Ptychopteridae, Trichoceridae, Anisopodidae, Tipulidae: Bulletin number 64. Connecticut Geological and Natural History Survey, Connecticut

Cummins KW, Klug MJ (1979) Feeding ecology of stream invertebrates. Annu Rev Ecol Syst 10:147–172

Dajoz R (2000) Insects and forests: the role and diversity of insects in the forest environment. Lavoisier, London

Dale MP, Causton DR (1992) The ecophysiology of *Veronica chamaedrys*, *V. montana* and *V. officinalis*. III. Effects of shading on the phenology of biomass allocations—a field experiment. J Ecol 80:505–515

Ehrlich J (1934) The beech bark disease, a *Nectria* disease of *Fagus*, following *Cryptococcus fagi*. (Baer.). Can J Res 10:593–692

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig D, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486

Eyre FH (ed) (1980) Forest cover types of the United States and Canada. Society of American Foresters, Washington, DC

Garnas JR, Ayres MP, Liebhold AM, Evans C (2011) Subcontinental impacts of an invasive tree disease on forest structure and dynamics. J Ecol 99:532–541

Gibbs JP (1998) Distribution of woodland amphibians along a forest fragmentation gradient. Landsc Ecol 13:263–268

Hane EN (2003) Indirect effects of beech bark disease on sugar maple seedling survival. Can J For Res 33:807–813

Hane EN, Hamburg SP, Barber AL, Plaut JA (2003) Phytotoxicity of American beech leaf leachate to sugar maple seedlings in a greenhouse experiment. Can J For Res 33:814–821

Healy WM, Brooks RT (1988) Small mammal abundance in northern hardwood stands in West Virginia. J Wildl Manag 52:491–496

Hewitt CG (1914) Note on the occurrence of the felted beech coccus *Cryptococcus fagi* (Baerens) Dougl. in Nova Scotia. Can Entomol 46:15–16

Houston DR (1975) Beech bark disease: the aftermath forests are structured for a new outbreak. J For 73:660–663

Houston DR (1994a) Major new tree disease epidemics: beech bark disease. Annu Rev Phytopathol 32:75–87

Houston DR (1994b) Temporal and spatial shift within the *Nectria* pathogen complex associated with beech bark disease of *Fagus grandifolia*. Can J For Res 24:960–968

Iason GR, Hester AJ (1993) The response of heather (*Calluna vulgaris*) to shade and nutrients—predictions of the carbon—nutrient balance hypothesis. J Ecol 81:71–80

Jakubas WJ, McLaughlin CR, Jensen PG, McNulty SA (2005) Alternate year beechnut production and its influence on bear and marten populations. In: Evans C, Lucas J (eds) Beech bark disease. Proceedings of the beech bark disease symposium. USDA-Forest Service, Gen Tech Rep NE-331, pp 79–87

Jones RH, Raynal DJ (1988) Root sprouting in American beech (*Fagus grandifolia*): effects of root injury, root exposure, and season. For Ecol Manag 25:79–90

Kirkland GL (1990) Patterns of initial small mammal community change after clearcutting of temperate North American forests. Oikos 59:313–320

Loo JD (2009) Ecological impacts of non-indigenous invasive fungi as forest pathogens. Biol Invasions 11:81–96

Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56: 395–405

Magurran AE (2004) Measuring biological diversity. Wiley-Blackwell Publishing, Malden

McGee GG (2000) The contribution of beech bark disease-induced mortality to coarse woody debris loads in northern hardwood stands of Adirondack Park, New York, USA. Can J For Res 30:1453–1462

McKenny HC, Keeton WS, Donovan TM (2006) Effects of structural complexity enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in northern hardwood forests. For Ecol Manag 230:186–196

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Morin RS, Liebhold AM, Tobin PC, Gottschalk KW, Luzader E (2007) Spread of beech bark disease in the eastern United States and its relationship to regional forest composition. Can J For Res 37:726–736

Muzika RM, Grushecky ST, Liebhold AM, Smith RL (2004) Using thinning as a management tool for gypsy moth: the influence on small mammal abundance. For Ecol Manag 192:349–359

Nyland RD, Bashant AL, Bohn KK, Verostek JM (2006) Interference to hardwood regeneration in northeastern North America: ecological characteristics of American beech, striped maple, and hobblebush. North J Appl For 23:53–61

Pearcy RW, Pfitsch WA (1991) Influence of sunflecks on the δ13C of *Adenocaulon bicolor* plants occurring in contrasting forest understory microsites. Oecologia 86:457–462

Pritchard G (1983) Biology of Tipulidae. Annu Rev Entomol 28:1–22

Rothstein DE, Zak DR (2001) Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. Funct Ecol 15:722–731

SAS Institute (2008) SAS/STAT 9.2 User's Guide. SAS Institute, Inc. Cary, NC, USA

Saunders DA (1988) Adirondack mammals. State University of New York, College of Environmental Science and Forestry, Syracuse

Semlitsch RD (2002) Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conserv Biol 16:619–629

Shigo AL (1972) The beech bark disease today in the northeastern U.S. J For 70:286–289

Somers RC (1986) Soil classification, genesis, morphology, and variability of soils found within the central Adirondack region of New York. State University of New York College of Environmental Science and Forestry, Syracuse, p 746

Storer AJ, Rosemier JN, Beachy BL, Flaspohler DJ (2005) Potential effects of beech bark disease and decline in beech abundance on birds and small mammals. In: Evans C, Lucas J (eds) Beech bark disease: proceedings of the beech bark disease symposium, Saranac Lake, NY. USDA Forest Service, Northern Research Station, Newtown Square, PA, p 149

Sydes C, Grime JP (1981) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: II. An experimental investigation. J Ecol 69:249–262

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474