

Subcontinental impacts of an invasive tree disease on forest structure and dynamics

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Summary

1. Introduced pests and pathogens are a major source of disturbance to ecosystems world-wide. The famous examples have produced dramatic reductions in host abundance, including virtual extirpation, but most introductions have more subtle impacts that are hard to quantify but are potentially at least as important due to the pathogens' effects on host reproduction, competitive ability and stress tolerance. A general outcome could be reduced host abundance with concomitant increases in the abundance of competitors.

2. Beech bark disease (BBD) is a widespread, fatal affliction of American beech (*Fagus grandifolia*), currently present in *c.* 50% of beech's distribution in eastern North America. Despite high adult mortality, beech remains a dominant component of the forest community.

3. Employing spatially extensive data from the national Forest Inventory and Analysis program of the United States Forest Service, we show that forests have changed dramatically in the presence of BBD. Within the 2.3 million km² range of beech, size-specific mortality was 65% higher in the longest-infected regions, and large beech (>90 cm diameter at breast height) have declined from *c.* 79 individuals km⁻² to being virtually absent. Small stem beech density was dramatically higher (>350%) such that infested forests contain a roughly equivalent cross-sectional (basal) area of beech as before BBD.

4. There was no evidence for compensation by sugar maple or other co-occurring tree species via increased recruitment or adult survivorship at the landscape scale. Overall, community composition remained roughly unchanged as a result of BBD.

5. Surprisingly, trajectory of stand dynamics (shifts in stem density and mean tree size reflecting normal stand maturation (self-thinning) or retrogression (more abundant, smaller trees over time)) did not differ between affected and unaffected regions. Variance in stand dynamics was greater in afflicted forests, however, indicating that predictability of forest structure has been diminished by BBD.

6. *Synthesis.* Forests of eastern North America have shifted to increased density and dramatically smaller stature – without notable change in tree species composition – following the invasion of a novel forest disease. Our results reinforce the conclusion that introduced diseases alter fundamental properties of ecosystems, but indicate that the spectrum of potential effects is broader than generally appreciated.

Key-words: beech bark disease, *Cryptococcus fagisuga*, disease impacts, *Fagus grandifolia*, forest ecology, Forest Inventory and Analysis, insect–fungal interactions, invasion ecology, *Neonectria ditissima*, *Neonectria faginata*

Introduction

Introduced organisms have powerful and rapidly expanding effects on ecosystem structure and function. Invasive species are regarded as among the top global threats to biodiversity,

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ecosystem resilience and adaptive capacity in the face of disturbance and global change (Vitousek *et al.* 1997; Wilcove *et al.* 1998; Olden *et al.* 2004). Forests are among the best-studied and globally important terrestrial ecosystems, owing to their extensive distribution, social, economic and aesthetic value, importance to biodiversity, and for their essential role as regulators of hydrologic, energetic and elemental cycles affecting many of Earth's systems, including climate (Bonan 2008). For several centuries, forests have sustained human-aided invasions by non-indigenous insects and pathogens, often with conspicuous consequences for forest structure and composition (Liebhold *et al.* 1995). Effects of such introductions include changes in ecosystem function (e.g. primary productivity, nutrient retention, hydrology, carbon storage, sensitivity to future disturbance), loss of forest diversity (including flora and fauna that depend on the affected tree species), changes in fire regime, disruption of competitive hierarchies and socio-economic costs associated with losses for forest-based industries (Liebhold *et al.* 1995; Ellison *et al.* 2005; Lovett *et al.* 2006; Ford & Vose 2007). The most notorious examples of invasive forest pests are those in which the affected tree species are effectively eliminated from the landscape, as happened to American chestnut following the introduction of the blight fungus (*Cryphonectria parasitica*) from Asia (Paillet 2002). However, few of the hundreds of non-indigenous herbivores and pathogens that have established in forests around the world (Pimentel 1986) have effects that are so easily characterized. It could be that many other invasive species are also altering forests but via impacts on stand dynamics that can only be recognized through analyses at such a large spatial scale that the appropriate data would be prohibitively expensive and time-consuming for any investigator to collect. We used data from the United States Forest Inventory and Analysis (FIA) program, a potentially powerful data set for testing hypotheses regarding the continental impacts of a widespread, invasive disease complex (beech bark disease, or BBD) on a dominant, foundational tree species (American beech – *Fagus grandifolia* Ehrl.) and associated forests in eastern North America.

Understanding the landscape effects of invasions on forest structure and function is vital in a world where humans are increasingly reliant on forests that are subject to accelerating human impacts (Dukes *et al.* 2009; Seppälä, Buck & Katila 2009). Spatially extensive studies are crucial for several reasons. First, many attributes of forests that matter to people (e.g. productivity, yield, carbon storage potential) are emergent properties of thousands of forest stands that cannot be meaningfully expressed at the level of individual plots at time-scales typical of most ecological studies (Orwig 2002). Secondly, undesirable declines in wildlife and biodiversity may be difficult to detect directly while there is still time for mitigation, but risks can be inferred from knowledge of forest structure across landscapes (Betts *et al.* 2006). Thirdly, understanding how local phenomena scale up is essential for land managers to apply knowledge from the wealth of studies that have been conducted at the scale of trees and stands (Holdenrieder *et al.* 2004). Traditional ecological studies have recognized the importance of considering nonlinearities and emergent proper-

ties that can only be studied at large spatial scales, but thus far progress has been hindered by the availability of appropriate data and analytical tools (Holling 1992; Levin 1992). The strength of this study is rooted in its large spatial extent, permitting inference about the effect of a non-native disease on forest structure and composition throughout the range of its host.

The ecology of BBD in North America is unique as it represents a case where the association between a non-native insect and endemic fungal pathogens has resulted in widespread forest disease. BBD is a pathogen complex of American beech (*Fagus grandifolia* Ehrl.) involving the European felted beech scale (*Cryptococcus fagisuga* Lind.) and several species of ascomycete fungi (primarily *Neonectria faginata* (M.L. Lohman, A.M.J. Watson & Ayers) Castlebury & Rossman and *Neonectria ditissima* (Tul. & C. Tul.) Samuels & Rossman; Houston 1994a; Castlebury, Rossman & Hyten 2006). *Neonectria* fungi exploit the feeding behaviour of scale insects to gain access to beech phloem resources, producing disease symptoms typified by localized cankering and associated necrosis on the bark, leading canopy dieback and elevated mortality risk (Ehrlich 1934; Houston 1994a). Since its introduction from Europe into Halifax, Nova Scotia, Canada, in the 1890s, populations of *C. fagisuga* have spread south and west, and currently encompass slightly < 50% of the range of beech in North America. It has been projected that BBD will eventually reach all 19 US States where beech occurs in substantial numbers (Morin *et al.* 2007). Several events of human-mediated jump dispersal have facilitated range expansion into North Carolina, West Virginia and, most recently, Michigan (Morin *et al.* 2007). Despite early predictions that beech would be extirpated by the disease, the species remains a dominant component of eastern forests (Twery & Patterson 1984; Leak 2006).

To evaluate the landscape-level impacts of BBD, we analysed a subset of FIA data (> 5500 plots from 15 of the 19 states with > 5% beech by volume) encompassing the range of the beech-containing forest in the United States. Four states were excluded because plot density was insufficient for analysis (see Materials and Methods for additional details about the FIA program). First, using data from the most recent complete inventory cycle available for each state, we tested for (i) departures from a stable size structure in beech and beech-dominated forests indicative of large-scale disease-induced forest disturbance (de Liocourt 1898); (ii) changes in size-specific mortality as a function of duration of infection with BBD; and (iii) compensatory regeneration by beech and co-occurring species. Secondly, by comparing over 2600 plots that were re-measured across FIA cycles, we tested the hypothesis that stand growth trajectory in beech-dominated regions invaded by BBD shifts from normal maturation (i.e. self-thinning; Yoda *et al.* 1963) to stand 'retrogression' – defined here as the accumulation of a greater density of small stems over time – relative to stands outside the current range of BBD. We used natural variation in the duration of infection to explore the temporal dynamics of disease impacts on stand structure and composition at the landscape scale. These two approaches yielded different but complementary information. Analyses based on

de Liocourt's Law compare static snapshots of forest size structure along a gradient of infection duration asking how size-specific mortality, equilibrium small stem density, and departure from the predicted pattern of approximate loglinearity (as a measure of large-scale disturbance) change as a function of disease. Analyses based on the self-thinning paradigm compare patterns in forest stand development in the presence vs. absence of disease, asking whether BBD-infected forests exhibit a mean trajectory skewed towards ongoing, cyclical replacement of fewer large stems with many small stems.

Materials and methods

For all analyses we used data from the FIA program collected by United States Forest Service. FIA data comprise tree- and plot-level measurements from more than 125 000 randomly selected plots, stratified by county and current land-use category, allowing statistically robust estimates of all forested area in the United States (Miles *et al.* 2001). We tested several *a priori* hypotheses regarding the effect of BBD on the structure and dynamic change of forest stands in the subcontinental landscape, encompassing much of the range of American beech. We employed these data in two ways: (i) assessing static tree size–density relationships of the forest and its component species, where departures from a stable size distribution are interpreted as evidence of widespread forest disturbance, and (ii) evaluating the direction of change in stand structure relative to predictions derived from a standard self-thinning curve, using FIA plots sampled two or more times in the last three decades, with 8–17 years between measurements. For both approaches, we compared observed patterns in the presence vs. absence of BBD and as a function of the time since the onset of BBD as reconstructed from historical records (Houston 1994a; Morin *et al.* 2007). We also considered estimates of dynamic structural change in the size–density relationship of trees within forest stands (termed 'stand trajectory') as a function of beech abundance (% beech basal area), initial stand stocking level, and presence vs. absence of BBD at the time of initial sampling. Throughout our analyses, we controlled for forest changes unrelated to BBD by comparing responses of beech with that of sugar maple as an ecological analogue that lacks the disease (Braun 1950; Poulson & Platt 1996).

STATIC STAND STRUCTURE AND DE LIOCOURT'S LAW

de Liocourt's Law (1898), since adapted and expanded (Meyer 1952; West, Shugart & Ranney 1981; Leak 1996; Manion & Griffin 2001; Munck & Manion 2006), predicts that forests at a stable size distribution will exhibit an approximately loglinear relationship between stem density and tree size, signifying a constant relative mortality per size class transition across all sizes of trees. By extension, large-scale disturbances that push forests away from equilibrium should be detectable as a departure from loglinearity (Manion & Griffin 2001). Further, the degree and shape of nonlinearity should provide clues to the type, duration and/or severity of disturbance. We constructed static life tables for beech and commonly co-occurring tree species in 15 states encompassing the range of beech using FIA data. While within the range of beech, New Jersey, Rhode Island, Kentucky and Florida were excluded from our analyses due to low numbers of usable beech plots. We also excluded all sites that were listed as partially or completely harvested in the FIA data base. This did not exclude plots where selection cuts took place. Data from a single sampling cycle per state were selected from the FIA data base to maximize the number of plots for each state (Table S1 in Supporting Informa-

tion). Comparing across states and FIA cycles is possible using regional extrapolations calculated from plot-level data, robust to differences in sampling design (Miles *et al.* 2001). Our analyses of static forest structure included 5521 plots containing a minimum of two beech stems larger than 10 cm diameter at breast height (d.b.h.; 1.4 m). Data were aggregated at the state level, except for New York and Maine, which we divided into multiple county regions (two and three regions, respectively) based on physical contiguity and common estimates for the date of arrival of scale insects (Table S1; see Appendix S1 in Supporting Information). For each common species and for all species pooled, we plotted the natural log of tree density vs. diameter class, and extracted slope and intercept estimates (\pm SE) from the first-order linear model. Slope estimates are interpretable as the average transition probability from one 2.54-cm-size class to the next, and were used to calculate baseline relative mortality rates under the assumption of a stable size distribution (Manion & Griffin 2001). To evaluate evidence for nonlinearities in the size–frequency data, we also fit models containing second- through fourth-order predictor terms and compared them using Akaike Information Criterion (AIC; Akaike 1974; Quinn & Keough 2002).

We matched each state/multicounty grouping (herein, 'region') with an estimated date of scale insect arrival, interpolated from historical reports (Table S1; Houston, Parker & Lonsdale 1979; Morin *et al.* 2007). For each region where BBD was present at the time of FIA sampling, we calculated the duration of BBD infection as the mean difference between the sampling year and the estimated year of scale insect arrival. To compare patterns in mortality rates and the equilibrium density of the smallest size class (estimated by the *y*-intercept) that might relate to BBD, we regressed each of these values against duration of BBD infection. Where appropriate, we used weighted least-squares regression to accommodate non-constant variance, using the inverse square of residual error from an OLS regression to serve as weights (Quinn & Keough 2002).

To test if minor departures from linearity uncovered in our initial analyses of static stand structure were related to BBD, we compared a total of six regression models containing higher-order d.b.h. terms and interactions with disease, regressed against the residuals from the linear model used to estimate size–density relationships across regions: $\log(\text{tree density}) = \text{d.b.h.} + \text{region} + \text{d.b.h.} \times \text{region} + \varepsilon$, where ε is the model error. Nested models built upon higher-order terms ('d.b.h.²' and 'd.b.h.² + d.b.h.³') were compared using AIC, either without interactions (two models), crossed with BBD presence/absence (two models), or crossed with the duration of BBD infection (two models). This procedure was repeated for all tree species combined, for beech and for sugar maple, allowing us to test for a systematic shift towards greater nonlinearity for beech and/or forests containing beech as a consequence of the disruptive effects of BBD to tree demography and a stable forest size structure, with sugar maple serving as a control.

DYNAMIC STRUCTURAL CHANGE IN REMEASURED PLOTS

To assess change in stand structure over time in the presence and absence of BBD, we calculated plot trajectories along a standard self-thinning curve (Fig. S1). Self-thinning refers to the dynamic process by which plant assemblages, in this case forest stands, decrease in stem density in a manner proportional to the overall growth of individual stems (de Liocourt 1898; Meyer 1952). Stands well below maximum biomass for a given site ('understocked' stands) are predicted to move towards the boundary line as trees grow and/or density increases via stem recruitment. Once at or near the boundary line,

stands typically begin to 'self-thin', becoming less dense through mortality of weak or suppressed trees that are out-competed for light and nutrients by dominant and co-dominant trees. Historically, researchers have hypothesized that the slope of the boundary line should be $-3/2$, a geometric relationship between the two variables with biomass (a cubic measure) on the y -axis vs. density (a squared measure) on the x -axis (White & Harper 1970). Accumulating empirical evidence and theoretical derivations invoking allometric scaling relationships now suggest that the slope of this line may be closer to $-4/3$, conforming to the widely reported population density–mass^{3/4} relationship, once the axes are inverted (West, Brown & Enquist 1997; Farrell-Gray & Gotelli 2005). The predicted trajectory for normal stand maturation for fully stocked stands is towards the upper left of the graph along the thinning curve boundary. Stands infected with BBD are likely to lose large adults, which may be rapidly replaced by seedlings or advanced sprout regeneration by beech, or by other species. Such an increase in density and decrease in mean diameter would correspond to movement to the lower right of the graph, which we have termed 'stand retrogression'. Thus, we predicted an increasing tendency towards stand retrogression where BBD is present, particularly as relative beech basal area increases. We estimated the slope and intercept of the biomass boundary line of the self-thinning curve using quantile regression. Quantile regression performs median regressions through each quantile of data points and is particularly useful where slopes and intercepts may vary across the data range, as is the case for estimating boundary slopes (Cade & Noon 2003; Koenker 2005). In this case, we used the 99th quantile ($\tau = 0.99$) to estimate the self-thinning boundary for each state individually and for all states pooled. Boundary line estimates using FIA data were similar across states, irrespective of BBD status, with an overall mean slope of -0.33 ± 0.03 SE (Fig. S1), closely matching theoretical expectations once we corrected for the use of a linear measure of tree size (diameter) rather than volume (Yoda *et al.* 1963; Enquist, Brown & West 1998). We then calculated stand trajectory as the linear distance parallel to the thinning curve boundary between each plot location on the graph at time t and time $t + x$, where x represents an intervening period between remeasurement cycles of 8 and 17 years, depending on state (Table S1). Movement relative to the boundary was centred on zero, with zero corresponding to either no change between cycles, or to movement orthogonal to the boundary line. Movement to the upper left (representing normal stand maturation, or self-thinning) was designated as positive, while movement towards the lower right (stand retrogression) was designated as negative. We categorized states as 'BBD present' or 'BBD absent' based on whether the estimated date of insect arrival preceded the first measurement cycle by > 10 years (conservatively approximating the time until arrival of *Neonectria* spp. and the onset of high mortality subsequent to the establishment of scale insects; Houston 1994b). We evaluated our predictions of an increasing tendency towards stand retrogression as the proportion of beech basal area increases (only where BBD is present) by testing for a negative slope in the lower boundary of the stand trajectory–percentage beech basal area relationship using quantile regression ($\tau = 0.05$) for plot with and without BBD (Fig. S2). We also constructed separate quantile regression models ($\tau = 0.05$) to test for an interaction between % beech and (i) BBD status and (ii) years since regional infection. Because the anticipated stand trajectory differs depending on stand stocking level, we also tested stand trajectory values detrended by proximity to the thinning curve boundary, by first regressing trajectory against the shortest distance of each plot to the boundary line and using the residuals for all subsequent analyses. This approach produced qualitatively identical results and was dropped for simplicity. Similarly, we tested for

differences in absolute magnitude of change from one cycle to the next as the Euclidean distance between paired points, as well as independent changes in both the mean diameter and mean trees per ha for each plot as a function of BBD status (Fig. S3).

DATA TREATMENT AND ANALYSIS

All data for static forest structure analyses, freely available at the USFS website (<http://www.fia.fs.us/tools-data>), were imported into Microsoft Access 2003, maintaining the relational structure of the data base as outlined in the FIA manual (Miles *et al.* 2001). Due to legal requirements to guard the anonymity of landowners, we acquired data for re-measured plot comparisons (for all plots with $> 2\%$ beech basal area) directly from the Forest Service, with all plot identifiers obscured. We used landscape-level extrapolations of tree density and mean tree diameter supplied by the USFS as indicators of local stand structure, thus avoiding potential problems arising from changes to sampling design across cycles or inexact relocation of previously measured trees. Summary data for both analyses were exported into R version 2.10.0 (R Core Development Team 2009) where all subsequent analyses were performed.

Results

STATIC STAND STRUCTURE AND DE LIOCOURT'S LAW

Among large, shade-tolerant species at structural equilibrium, tree density declined approximately loglinearly with size class in all regions (see Fig. 1 for a randomly selected state/region; full regression models for beech, sugar maple and all species combined were as follows: $F_{35,506} = 308.6$, $P < 0.00001$, $R^2 = 0.96$; $F_{35,452} = 189.7$, $P < 0.00001$, $R^2 = 0.94$; $F_{35,638} = 490.1$, $P < 0.00001$, $R^2 = 0.96$). This relationship, known as de Liocourt's Law (1898), arises when forests are at approximate structural or demographic equilibrium because it is common for the probability of growing into the next size class to be approximately constant across size classes (when data are aggregated at a large enough spatial scale to average over local disturbances; Manion & Griffin 2001). Beech, sugar maple and all species pooled showed broad visual correspondence with first-order models in all regions, irrespective of BBD (Fig. 1a–c). As expected for an early successional, shade-intolerant species, paper birch departed substantially from loglinearity, with declining probabilities of larger trees reaching the next size class (Fig. 1d). In no case did the inclusion of higher-order terms improve model variance explained by more than 1–2% for beech, sugar maple or all species combined. Thus, beech and beech-containing forests were roughly at structural equilibrium throughout the range of the species, and we reject the hypothesis that BBD is strongly evident as a large-scale disruption in mortality schedules relative to a stable stage distribution.

The effects of BBD were most clearly visible in the FIA data as dramatic shifts in transition probabilities among size classes and in the estimated equilibrium small stem density. Size-specific mortality increased approximately linearly for beech with time since regional infection ($F_{1,16} = 39.2$; $P < 0.0001$; $R^2 = 0.71$; Fig. 2a). This trend, corresponding to progressively

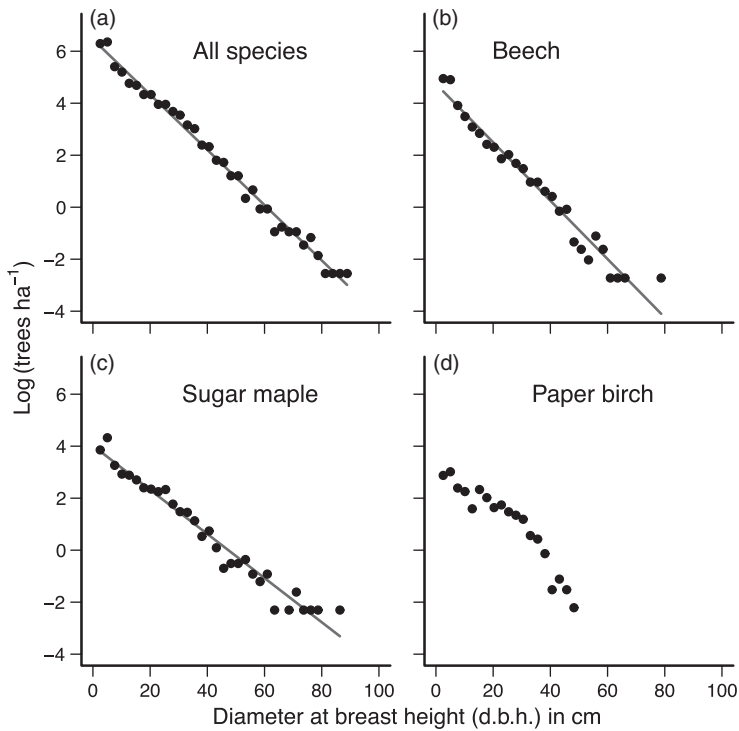


Fig. 1. Size–density relationships for New Hampshire forests (randomly selected from states affected by beech bark disease) for all species combined (a) and for beech (b), sugar maple (c) and paper birch (d). Fitted lines are first-order ordinary least-squares regression lines. The relationship for paper birch is best approximated by a third-order nonlinear model, conforming to expectations for an early successional, shade-intolerant species where mortality rate spikes at the onset of light competition (shown for contrast).

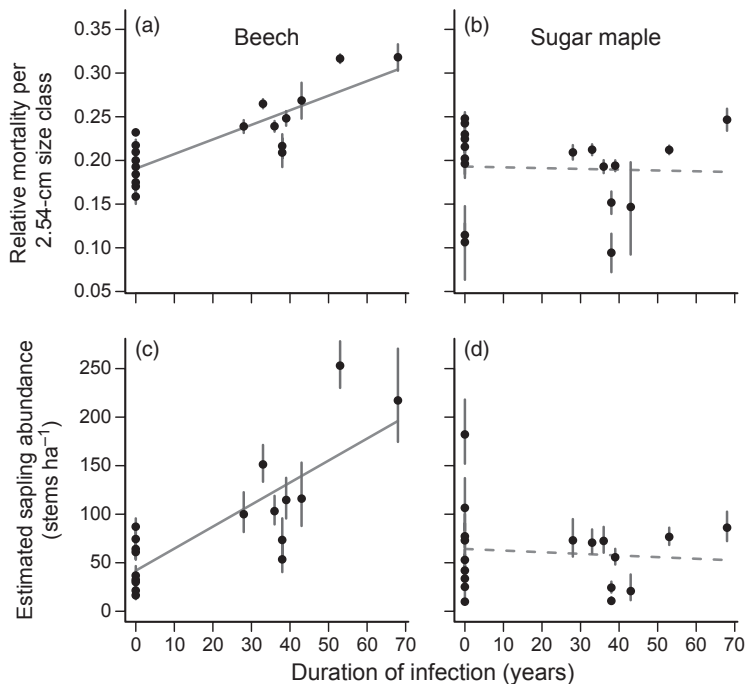


Fig. 2. Baseline relative mortality per size class under a stable stage distribution (upper panels), and estimated sapling abundance per ha (lower panels), as a function of the duration of infection with beech bark disease (BBD). Left panels correspond to beech and the right panels to sugar maple. Points (± 1 SE) are mean values for each state/multicounty region considered. Sugar maple was selected *a priori* as an ecological analogue to beech that is not directly influenced by BBD.

steeper negative slopes in the size–density relationship (as in Fig. 1) since BBD was detected, equates to a shift in relative mortality rate per 2.54-cm-diameter class from a mean of 19.3% in areas with no history of BBD at the time of measurement to 31.8% in the longest-affected forests (Fig. 2a). As expected if the effect were due to BBD, baseline relative mortality for sugar maple was similar to that of beech in uninfected forests (19.1%), and showed no pattern with time since

BBD infection (Fig. 2b). For beech, the predicted average number of stems per hectare in the smallest size category increased significantly with time since infection ($F_{1,16} = 29.7$; $P < 0.0001$; $R^2 = 0.65$), reflecting up to a 362% increase (from 47 to 217 stems ha^{-1} ; Fig. 2c). For sugar maple, equilibrium small stem density was similar across regions, and there was no pattern with respect to duration of BBD infection (Fig. 2; $\bar{x} \pm \text{SE} = 61 \pm 10$ stems ha^{-1}).

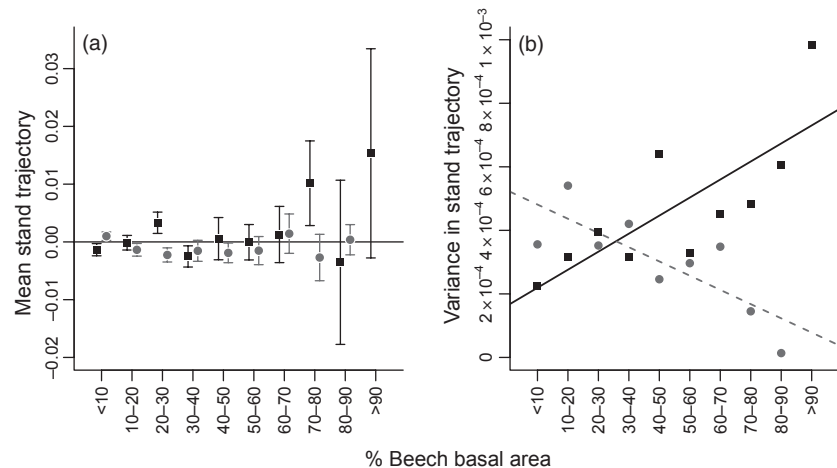


Fig. 3. Mean (\pm SE) (a) and variance (b) in stand trajectories vs. beech abundance. Black squares and grey circles denote presence and absence of beech bark disease, respectively. Stand trajectory was quantified as movement parallel to the thinning curve boundary, where positive values denote maturation or normal self-thinning (fewer, larger stems over time) and negative values denote stand retrogression (more abundant, smaller stems over time). See Materials and Methods for details.

It is not logically possible for there to be marked increases in size-specific mortality rates from BBD without transient dynamics in size structure (departures from de Liocourt's Law) associated with the passage of the advancing front of BBD infection. The signal of these transient dynamics was weak. Within regions, a model of constant transition probabilities for beech between size classes (following de Liocourt's Law) accounted for 96% of variation in the relationship between $\log(\text{density})$ and size. However, further analyses revealed that the modest departures from linearity covaried with BBD (Fig. S4; Table S2). The best supported higher-order models for beech, but not for sugar maple, contained both second- and third-order d.b.h. terms as well as interactions with duration of infection with BBD (Table S2). As expected, the best nonlinear models showed a progressive surplus of small stems and under-representation of large trees with increasing duration of infection (Fig. S4).

DYNAMIC STAND TRAJECTORY

Self-thinning, a foundational principle in plant population ecology, describes the process by which plants within a stand tend to increase in average stem size while decreasing in density (Yoda *et al.* 1963). BBD favours decreases in mean size and increases in density by effectively replacing large, mature trees with sprouts and seedlings (Houston 1994b). Thus, movement along the thinning curve boundary in mature, infected stands was predicted to be opposite that of normal self-thinning, potentially in a recurring cycle as small stems produced at the time of canopy tree dieback age into susceptibility. Contrary to this prediction, BBD did not alter the mean direction of change relative to the thinning curve boundary in remeasured plots. Stands that self-thinned during the 8–17 years between measurements were as common as those proliferating smaller stems, irrespective of beech density and disease status (Fig. 3a). Lower quantile slopes ($\tau = 0.05$) did not differ from zero where BBD was present ($CI_{95\%} = (-0.003, 0.002)$) or absent ($CI_{95\%} = (-0.005, 0.002)$), nor were there significant interactions with BBD presence/absence ($F_{1,2625} = 0.07$; $P = 0.79$) or time since infection ($F_{1,2625} = 0.06$; $P = 0.81$) when these terms were included in models (Fig. S2).

We therefore rejected the hypothesis of broad scale, disease-induced cyclical replacement by smaller stems in beech forests. However, variance in stand trajectory increased significantly with percentage beech basal area per stand in regions with BBD ($F_{1,8} = 11.9$; $P = 0.009$; $R^2 = 0.60$; Fig. 3b), and decreased where BBD was absent ($F_{1,7} = 12.2$; $P = 0.01$; $R^2 = 0.63$), indicating that growth trajectories of forests dominated by beech are less predictable in the presence of BBD.

Discussion

Analyses of FIA data from the eastern United States showed clear effects of BBD. Our results demonstrate greatly increased size-specific beech mortality and compensatory recruitment by small beech. The magnitude of this effect increases approximately linearly with the duration of BBD infection in a region, up to 68 years prior to sampling in the longest-affected region in the United States (northern Maine). Two main hypotheses concerning the role of BBD in forest ecosystems were not supported, namely that BBD produces a lasting, large-scale perturbation away from a stable size structure of stems, and that BBD dynamics are characterized by cyclical replacement of large stems with smaller stems at a decadal time-scale. The goodness-of-fit for de Liocourt models of beech within infected regions was comparable to analyses of other forests that appeared to be at or near structural equilibrium (see West, Shugart & Ranney 1981). The only signal of BBD disturbance from the de Liocourt analyses was a weak tendency for departures from de Liocourt's Law to covary with time since BBD infection. This presumably reflects transient dynamics from one survivorship schedule (pre-BBD) to another (following establishment of BBD), but could also reflect regional differences in harvesting regimes or tendency for adventitious root sprouting (Kitamura & Kawano 2001; Fig. S4).

Another surprising result from analyses of FIA data was the lack of compensatory recruitment in the wake of BBD by tree species that co-occur with beech. There was in fact a vigorous response in the regeneration layer, but that response was predominantly by beech itself. Part of this robust compensatory response by beech has undoubtedly to do with the species' propensity to reproduce vegetatively via adventitious root sprouts,

especially from damaged root systems (Jones & Raynal 1988). The capacity to resprout from long-lived root systems is responsible for the maintenance of American chestnut as an understorey shrub in the presence of Chestnut blight (Paillet 2002). Indeed, vegetative reproduction may be a general mechanism promoting species persistence in the face of strong biotic threats. Unlike chestnut, whose sprouts quickly become reinfected soon after breaking the soil surface (Paillet 2002), many beech sprouts and seedlings survive long enough to reach the canopy, owing to extended ontogenetic immunity to scale insect attack and to relatively slow disease progression on infected stems (Houston 1994a). Perhaps counterintuitively, this pattern of intermediate tree longevity (uninfected beech live longer than infected beech, which live much longer than chestnut sprouts) may be as consequential to forest structure and function as outright species removal from the canopy, as occurred with chestnut. The full range of impacts stemming from the loss of chestnut from eastern forests may never fully be understood, but clearly tree communities proved resilient to species removal, as chestnut was quickly replaced by a variety of species, largely oak, hickory and hemlock (Loo 2009). By contrast, beech still competes strongly at all life stages and remains a dominant component of the forest canopy, but altered demographic rates in the presence of BBD has led to a new equilibrium condition marked by denser, smaller forests.

Beech longevity in the presence of BBD also has consequences for evolutionary responses to the disease. In contrast to chestnut, which now very rarely survives to reproduce sexually, many beech survive to flower and produce seed. Sexual reproduction, in combination with some heritable variation in susceptibility to BBD (Koch *et al.* 2010), may permit the evolution of increasing resistance and reduced disease impacts over time.

To our knowledge, this article is the first to test hypotheses concerning the effects of an invasive disease throughout the range of a broadly distributed host, in this case within the whole of the eastern North American deciduous forest. Outcomes of this study have application beyond improved understanding of the impacts of BBD for two basic reasons. First, results highlight an important but generally underappreciated effect of invasion – in this case the dramatic alteration of forest size and age structure with little or no concomitant change in species composition. Secondly, our results validate the use of a large, taxpayer-funded data base such as the FIA to test *a priori* hypotheses that would otherwise be intractable using traditional experimental and observational approaches. The data produced by the FIA program were sufficiently concordant with expectations from forest dynamics theory that it was legitimized as a tool for assessing impacts from new agents of disturbance.

The most compelling evidence for broad impacts of BBD on forest structure was the dramatic increase in size-specific beech mortality as a function of how long a region had been infected with BBD. These effects are strong enough to produce notable changes in the abundance of large trees in a forested landscape. Extrapolations from FIA data predict an equilibrium density of *c.* 79 beech km⁻² with > 90 cm d.b.h.

in uninfected forests, whereas in the longest-infected forests (> 50 years with BBD), an average square kilometre should not contain a single beech > 90 cm d.b.h., and only 14 stems > 60 cm d.b.h. The lack of divergence from a loglinear survival model further indicates that mortality rate is approximately constant across size classes, which contradicts earlier reports that BBD strikes primarily larger size classes, although this is undoubtedly true in the earliest stages of stand infection along the advancing front of the disease (Houston 1994b). Slower radial growth associated with BBD (Gavin & Peart 1993) may result in a slower cycling rate from one size class to another but should not influence the long-term stable age distribution. Another striking result that emerged from our analyses is that there was no sign of compensatory increases in survival of other important hardwood trees such as sugar maple. Similarly, there was no evidence for increased reproduction or seedling survivorship of co-occurring tree species (Fig. 2d; results for other common species were qualitatively similar), presumably because the density of small beech has increased so dramatically with BBD. Based on other research, it is clear that in given stands and regions species composition has changed as a possible consequence of BBD (Griffin *et al.* 2003), but at a landscape scale, it appears that beech is predominantly replacing itself. Thus, BBD is altering North American hardwood forests to a condition where trees are of generally smaller stature (because BBD kills mature beech trees) but with no decline in the space occupied by beech. This result joins a growing list of cases where complex interactions between disease organisms and host plants disrupt competitive hierarchies leading to unanticipated changes in the relative densities of affected species (Power & Mitchell 2004; Cobb, Meentemeyer & Rizzo 2010). To date, however, such examples involve apparent competition linked to generalist pathogen spillover on differentially susceptible hosts; BBD represents the first case that we know of where a specialist plant pathogen actually increases the density of its host. As a result of the shift to smaller, denser stands of beech, hardwood forests of North America contain dramatically fewer large trees than before invasion by BBD. Perhaps most importantly, this does not seem to be a case of transient dynamics that forests are likely to grow out of, but rather a self-reinforcing condition that is maintained because increased regeneration of the afflicted tree species balances elevated mortality from the disease. While moderate, increasing departures from linearity in the size–density relationship for beech and for the forest as a whole show a gradual shift towards a greater surplus of small stems and dearth of large trees as duration of infection increases, even relative to the dramatically steepening survival curves along the same temporal gradient. The current trajectory implies that forests will continue to contain an abundance of both beech and BBD for the foreseeable future.

Our analyses of stand dynamics across 8–17 year intervals indicated that BBD is not changing the probability that stands mature (self-thin) vs. retrogress (tend towards smaller stems at higher densities) at that time-scale. Data matched across FIA cycles were subject to additional sources of error

relative to data from individual cycles. For example, some variability was probably introduced due to imperfect relocation of plots or to changes in plot design across cycles in some regions. However, we avoided some potential bias by using extrapolations from the data ('expansion factors' calculated by the FIA program) instead of tree counts, and interpret the data as stand averages rather than attempting to directly compare plot- or tree-level estimates from one cycle to the next. The validity of the matched data is supported by concordance with expectations from plant community theory. Our estimates of the thinning curve boundary showed surprising correspondence with theoretical predictions, although slope estimates were slightly outside the range of statistical equivalence (theoretical estimate = -0.375 , empirical slope $CI_{95\%} = (-0.36515, -0.22969)$; Fig. S1). The modal stand condition (from Fig. S3) was *c.* 390 stems ha^{-1} with an average diameter of about 25 cm. As expected due to the pressures of self-thinning (namely competition for light and nutrients), the frequency distribution of tree size vs. density was sharply truncated at the upper edges but had a relatively long tail of stands with lower combinations of density and size. Stands exhibited a wide range of stocking levels; *c.* 33% of plots was understocked (at or below $14\text{--}17\text{ m}^2\text{ ha}^{-1}$ for a similar forest type, depending on stem density; Gingrich 1967). Thirty-nine per cent of stands was 'fully stocked' (between $14\text{--}17$ and $24\text{--}34\text{ m}^2\text{ ha}^{-1}$); the remaining 28% was overstocked under this classification scheme. Self-thinning is expected to be a meaningful force in stands that are fully stocked, or especially overstocked, but less so where cross-sectional (basal) area is low. Patterns in the direction of stand change over time as well as our estimates of the thinning curve boundary were qualitatively similar irrespective of whether we excluded understocked stands or accounted for stocking levels by using proximity to the thinning curve boundary as a covariate in our analyses. As expected, highly stocked stands, constrained by processes of self-thinning, were not observed to gain both stems and mean diameter, but all other trajectories were approximately equally likely, including a loss of basal area between measurement cycles. This pattern, coupled with the large proportion of stands with low stocking, suggests that local disturbance is a driving factor in forest dynamics, even over relatively short time-scales. Similarly, there was no strong pattern in directional change in understocked stands; *i.e.* relocated plots did not inevitably mature towards full stocking in the 8–17 years between cycles. Because this is a statistically rigorous random sample of the region, we take our data to be indicative of how the thinning curve looks in a random sample of stands across a large landscape.

An intriguing and potentially significant result from our analyses of dynamic trajectory is that BBD invasion has made the trajectories of beech-containing stands less predictable relative to uninfected stands (Fig. 3b). The mechanisms for more variable stand dynamics could not be specified with the data at hand, but probably include human responses to the disease via altered harvesting practices (Yoda *et al.* 1963; Holling 1992). Regardless of the cause, this pattern of increased variance in

the presence of BBD has broad implications since it adds uncertainty to models of forest growth and yield for harvesting, wildlife management and carbon sequestration, among others.

Such a dramatic change in the size structure of trees has inevitable direct and indirect consequences for forest structure and function and for human interactions with forest systems. The loss of large trees reduces habitat for many species that are already scarce due to extensive harvesting and land conversion (*e.g.* canopy-nesting birds, birds and mammals that exploit tree cavities, epiphytic communities and saproxylic invertebrates that are adapted to large-diameter woody debris; Hunter 1999; Burdon, Thrall & Ericson 2006). BBD-infected forests contain fewer and smaller beech that are reproductively mature, reducing seed mast (beechnuts), which is a critical food resource for many birds and mammals (Ellison *et al.* 2005). Coarse-scale canopy complexity is reduced by the loss of large, dominant trees (canopy emergents), which can influence elemental flux rates with the atmosphere (Lovett, Reiners & Olson 1982; Ellison *et al.* 2005). Increased competition for light and space from increased density of small beech limits the abundance and diversity of plant species that are adapted to the understorey of mature forests, including scores of spring ephemerals that are indigenous to eastern North America (Schemske *et al.* 1978). High densities of small beech, relatively unpalatable to vertebrate herbivores, reduce food resources for browsing mammals and amplify grazing pressure on more palatable species (Nyland *et al.* 2006; Feng *et al.* 2009). More rapid turnover of beech increases the supply rate of dying woody tissue to species such as ambrosia beetles, borers, wood wasps and decay fungi, which normally function as early successional saprophytes but can begin attacking healthy plant tissue, including other hardwood species, when they become locally abundant (Feng *et al.* 2009). The most dramatic regional impacts of BBD, however, are likely to arise from changes in interactions between humans and forests. Decreased abundance of large trees generally decreases the probability of harvesting, but not necessarily for American beech, which has never been highly valued for lumber or veneer. Conversely, BBD can provide an incentive in managed forests for harvesting younger trees for pulp (before incurring losses due to BBD). Perhaps most importantly, stands of dense, small-stemmed beech may tend to be candidates for conversion to land for agriculture, housing or other non-forest land uses. This is in contrast to stands of strikingly old large beech trees, widely appreciated for their aesthetics and increasingly preserved for that reason (Peattie 1991).

The last century has seen a vast natural experiment playing out over eastern North America due to the emergence of BBD. In addition to being significant in itself, this provides a case study regarding changes in forest structure and function in the face of novel forest disease. Our results demonstrate the need for a broad spatial and temporal perspective in understanding disease impacts on ecosystems. The combination of late disease onset and the strong capacity for host regeneration facilitate long-term persistence of beech despite greatly elevated mortality. Unlike chestnut blight and other notable forest diseases,

the importance of BBD to forest structure and ecosystem function arises not via local or regional host extirpation but from a dramatic alteration in the life history of a foundation tree species.

Biological invasions are already among the most globally powerful drivers of uncontrolled changes in ecosystems and unintended losses of ecosystem services (Mack *et al.* 2000). The challenge of biotic invasions to ecosystems and natural resource managers will probably grow as propagule pressure accelerates with globalization and invasibility increases with climate and human land-use change (Walther *et al.* 2002; Theoharides & Dukes 2007; Pauchard *et al.* 2009). Traditional options for strategic responses (prevention, eradication, mitigation) are costly and wrought with technical challenges. Effective decision-making requires rapid growth in our empirical and theoretical understanding of invasion impacts. Our analyses reveal that the diversity of potential impacts is greater than generally appreciated. A novel disease complex such as BBD can profoundly alter the size structure of forests and decrease the predictability of forest dynamics without reducing the abundance of its host, even as those forests lose the traditional signature of a disturbed forest (departures from de Liocourt's Law). The nature of these impacts highlights the need for long-term, spatially extensive environmental inventories and monitoring programmes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Beech bark disease and forest structure SI.

Table S1. Summary of Forest Inventory and Analysis data used in static life table construction, with estimated year of scale insect establishment.

Table S2. Summary statistics from model selection evaluating departures from loglinearity in de Liocourt tree size–log(density) relationships for all species, beech and sugar maple, with and without beech bark disease (BBD) terms.

Figure S1. Self-thinning curve estimated from Forest Inventory and Analysis data for beech-containing forest plots in the 15-state study area.

Figure S2. Left: Stand trajectories (with respect to the self-thinning curve) as a function of relative beech abundance for Forest Inventory and Analysis plots and beech bark disease status, for beech and sugar maple. Right: Regression slope estimates by quantile (τ), with 95% confidence intervals.

Figure S3. Mean tree diameter and stem density for states by presence/absence of beech bark disease at the time of first measurement.

Figure S4. Patterns of nonlinearity in residual variation around regional size–density relationships by duration of beech bark disease infection, for all species combined, beech, and sugar maple.

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