

RESEARCH ARTICLE

Functional traits contribute in opposite directions to taxonomic turnover in northeastern US forests over time

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Abstract

Aims: Understanding the processes driving forest dynamics requires considering that species within communities do not respond in a coordinated manner to external factors. We argue that temporal turnover in species composition results from contrasting differences in species life history and functional strategies (demography and seed and wood traits) that might simultaneously promote stability and dynamism by operating on distinct subsets of species. Specifically, fast taxonomic turnover should be promoted by species that take advantage of sporadically available resources, while forest stability should be promoted by species with conservative and stress-tolerant life histories.

Location: Northeastern USA.

Methods: We combine demographic information (survival, recruitment) over a 14-year period from temperate tree communities in the northeastern United States with trait information on species seed mass and wood density as a proxy for their reproductive and resource acquisition strategies, to evaluate the differential contribution of species with contrasting ecological strategies (low vs high seed mass/wood density) to rates of compositional turnover in temperate forests.

Results: The apparent dynamism of US forests is mostly driven by high mortality and low recruitment of small-seeded species and by high mortality and recruitment of low wood density species. Simultaneously, species with the opposite traits, i.e., high seed mass and wood density, contribute more to stability. Our findings suggest that forests dynamics in the northeastern United States are the outcome of opposing contributions of life history and plant traits that simultaneously promote forest stability and rapid taxonomic turnover by operating differentially across tree species.

Conclusions: Small-seeded and low wood density species promote faster forest turnover than species with the opposite traits. Not accounting for these functional differences in community-level analyses is likely to mask the complex dynamics of temperate forests. This study demonstrates the importance of studying forest composition and structure under a dynamic scope that accounts for differences in functional strategies across species.

KEYWORD

community diversity, community dynamics, seed mass, temperate tree communities, temporal turnover, wood density,

1 | INTRODUCTION

Understanding plant community dynamics – shifts in taxonomic and functional composition over time – is needed for predicting forest changes, a critical matter under current and projected climatic scenarios (Parmesan & Yohe, 2003). Addressing this issue, however, is particularly challenging because multiple drivers, including climate, pests, and disturbance, simultaneously operate on forest communities and may have opposing effects on floristic composition. For instance, a recent study in the forests of North America suggests that changes in climate are favoring drought-tolerant over drought-intolerant species (Trugman et al., 2020), yet successional processes in these same forests are simultaneously benefiting the establishment of early/mid-successional species, which tend to underperform in conditions of low water availability (Chapman & McEwan, 2016). Similarly, while climatic conditions might favor the establishment of species able to cope with new stresses, species-specific pests might heavily impair the performance of some of these species (Abrams & Mostoller, 1995). These conflicting responses may nullify each other resulting in a net outcome that does not reveal all the complexity of processes driving forest dynamics, and thereby imposing important challenges for predicting the fate of today's forests. For temperate forests in the United States, it is well known that species may respond idiosyncratically to different factors (Davis & Woods, 1989; McEwan et al., 2011; Sprugel, 1976). Reaching a synthetic understanding of shifts in community composition requires moving beyond the notion that plant dynamics are an aggregated and coordinated change in species composition over time toward a more individualistic view of dynamics where species have different contributions to temporal turnover (Gleason, 1926).

Forest dynamics can be described as the outcome of differences in life history and ecological strategies across species that simultaneously promote either rapid change or stability. On one hand, fast taxonomic turnover can be promoted by species that can take advantage of sporadically available resources and that are often transient members of the community. On the other hand, other species may promote stability and act as core components of communities, being more resistant to climatic changes, disturbance, and environmental uncertainties (Thompson et al., 2013). Accounting for differences in terms of resource use and reproductive strategies across species should allow to identify those that enhance floristic stability and those that promote dynamism (Coyle et al., 2013; Norden et al., 2017; Snell Taylor et al., 2018; Umaña et al., 2017; Wang et al., 2018). For instance, species characterized by short life spans and acquisitive resource-use strategies are expected to take advantage of pulses in resource availability and, thereby, should contribute more to fast dynamics (high recruitment and/or low survival rates), representing more transient community components. In contrast, species

characterized by long life cycles and conservative resource-use strategies should exhibit more stable dynamics and represent core components of the community (low recruitment and/or low survival rates).

To gain further insight into the complexity of forests' community-level temporal taxonomic turnover, we propose to identify the relative contribution of different tree species to forest dynamics, depending upon their functional traits – morphological and physiological attributes that influence the interaction between an organism and its surrounding environment (Arnold, 1983; McGill et al., 2006; Violle et al., 2007). Seed size and wood density show important variation across species (Díaz et al., 2016; Westoby, 1998) and are critical traits determining plant demography and ultimately forest dynamics (Adler et al., 2014; Chave et al., 2009). In particular, seed mass represents a trade-off between producing many small, stress-intolerant seeds or few large, stress-tolerant seeds (Muller-Landau, 2010; Rees, 1995; Turnbull et al., 1999; Westoby et al., 1992). Small-seeded species are recognized to have good colonization abilities as they can disperse widely and have high potential rates of per capita seedling recruitment, but may fail to persist in older size classes due to their low stress tolerance (Coomes & Grubb, 2003; Everham et al., 1996; but see Moles, 2018). In contrast, large-seeded species are stress-tolerant, which in turn leads to high survival rates yet accompanied by low seedling recruitment due to low per capita seed production (Muller-Landau, 2010). Similarly, variation in wood density reflects differences in a range of ecological strategies in which high wood density species tend to have long life spans and conservative resource-use strategies, while low wood density species typically exhibit short life cycles and are characterized by acquisitive resource-use strategies (Osazuwa-Peters et al., 2017; Wright et al., 2010). In brief, small-seeded and/or low wood density species, associated with fast demography (either low survival or high seedling recruitment), are expected to contribute to rapid turnover in taxonomic composition over time, while large-seeded and/or high wood density species, which exhibit slow demography, are expected to contribute to taxonomic stability.

In this study, we evaluated the role of traits promoting either dynamism or stability in tree species in temperate forests. We examined patterns of tree species turnover across 1053 forest plots monitored over a 14-year period in the northeastern United States. The forests in this region are at different successional stages and are currently undergoing shifts in species composition and dominance due to variable disturbance history, abiotic factors, climatic factors, and diseases (Abrams & Nowacki, 1992; Bürgi et al., 2000; Thompson et al., 2013). We hypothesized that small-seeded and low wood density species contribute to rapid changes in community composition over time, while large-seeded and high wood density species contribute to taxonomic stability. These patterns should be the result of different demographic

processes where taxonomic turnover driven by small-seeded species and low wood density species may occur through high recruitment and/or low survival of these species. Specifically, we asked: (1) what is the contribution of species with different seed sizes and wood densities to patterns of turnover in community composition; and (2) how do demographic rates (i.e., recruitment and survival) of species with distinct seed size and wood density values explain differences in temporal turnover at the community level?

2 | MATERIALS AND METHODS

2.1 | Survey data

We used data from the Northeast USA Forest Inventory and Analyses database (FIA) that included local tree communities across 13 states (Connecticut, Delaware, Maine, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, and West Virginia). We selected communities monitored from 2001 to 2014 across 1053 permanent plots (three census periods per plot) and including 25 tree species. Each plot consisted of four circular subplots with a 7.32 m fixed radius and separated by 36.6 m. Within each plot, all trees with a diameter at breast height (DBH) >12.7 cm were tagged, identified, and monitored for survival. We used subplots as our sampling unit for all the analyses. We included plots that fulfill the following conditions: (1) plots measured at least twice; (2) no evidence of logging since the last measurement; (3) no evidence of damage by insects, disease or fire since the last measurement; and (4) closed-canopy forests that included plots established in forested land (with at least 10% cover by live trees of any size). Agriculturally managed areas such as fruit orchards, or land areas in urban sites such as city parks were not considered in this study (Miles et al., 2001). The selected plots represented closed-canopy forests in the northeastern United States that have not been disturbed in the recent past (2000–2014) but could have been disturbed before the studied period representing secondary forests.

2.2 | Trait data

We compiled information on seed mass (mg) and wood density (g cm^{-3}) from the Seed Information Database (SID) from the Kew Royal Botanic Gardens webpage (<http://data.kew.org/sid/>) and the Global wood density Database webpage (<https://datadryad.org/stash/dataset/>, <https://doi.org/10.5061/dryad.234>), respectively. Both traits were moderately correlated ($r = 0.5$, $p = 0.02$, Appendix S1) and were not related to species abundance (Appendix S1).

2.3 | Analyses

We evaluated changes in taxonomic similarity for each subplot over 14 years (temporal turnover) by calculating similarity in species

composition between consecutive censuses based on Hill numbers using as a reference point the species composition in the first census. This way, we obtained a trajectory for each plot composed of two similarity values. Hill numbers represent the effective number of species, in other words, the number of equally abundant species needed to get the same diversity value (Chao et al., 2014a). Although Hill numbers have been typically used to evaluate alpha diversity, they can also serve to measure taxonomic similarity. Specifically, to compare pairs of assemblages (e.g. $subplot_i$ at census 1 and $subplot_j$ at census 2), Hill numbers of the pooled assemblages (gamma diversity) were decomposed into independent alpha and beta components of diversity and monotonically transformed into similarity measures (Chao et al., 2014a). These indices are more appropriate than other commonly used metrics because they obey to the replication principle (linearity with respect to increases in diversity) (Chao et al., 2014b; Jost, 2006; Jost et al., 2011). We used three similarity metrics that differentially weight species abundance (number of individuals). The incidence-based Sørensen index, and the abundance-based Horn and Morisita–Horn indices, give values for subplot floristic similarity between time t_0 and time t_n , where n represents the year when a specific tree community was re-censused (Chao et al., 2014a). We selected t_0 as the reference point to be able to compare changes in taxonomic similarity over time. The Sørensen index weighs all species equally, while the Horn index weighs each species based on their relative abundance (Horn, 1966; Jost et al., 2011). The Morisita–Horn index is more sensitive to dominant species, while the Horn index is more susceptible to the abundance of rare species (Jost et al., 2011).

To examine the contribution of species seed mass and wood density to taxonomic turnover over time, we performed a sensitivity analysis evaluating the effect of removing subsets of species depending on their morphological traits in temporal species turnover, following Norden et al. (2017). To do so, we first classified all species using bins (Appendix S1). *Bin-2* separated species into two categories by keeping a similar number of species in each category (small- and large-seeded species: 12 and 13 species respectively; high and low wood density species: 12 and 13 species respectively; Appendix S1). *Bin-3* separated seed mass into three categories (small, medium and large) based on differences in orders of magnitude (small: 0–<10 mg [nine species], medium: 10–<100 mg [nine species] and large: ≥ 100 mg [seven species]; Appendix S1). For wood density, given that the total range of variation in this trait did not cover several orders of magnitude as for seed mass, the *bin-3* classification was performed to keep a similar number of species in each of the three categories (low wood density: seven species, medium wood density: eight species, high wood density: nine species; Appendix S1). Once these classes were defined, we recalculated, for each subplot, taxonomic similarity between t_0 and t_n over the 14 years following removal of each of these groups of species, one at a time (e.g., $ALL_{w/o\ LSM}$ excludes species with large seed mass; $ALL_{w/o\ MSM}$ excludes species with medium seed mass; $ALL_{w/o\ SSM}$ excludes species with small seed mass) and obtained a new trajectory of similarity values over the studied time period (14 years) for each data set.

We then compared temporal turnover, as measured in similarity values between consecutive censuses, for the whole community (that is, including all species within each subplot: ALL) to patterns obtained when removing subsets of species belonging to groups characterized by their seed size and wood density, separately. For example, for each subplot, we compared the trajectory describing temporal turnover based on the whole community (ALL) to that obtained when removing large-seeded species ($ALL_{w/o LSM}$; Figure 1). We then repeated this procedure for all the categories of the two bins (e.g., for *bin-2* and seed mass: ALL vs $ALL_{w/o LSM}$, ALL vs $ALL_{w/o SSM}$; for *bin-2* and wood density: ALL vs $ALL_{w/o LDW}$, ALL vs $ALL_{w/o HWD}$). Next, we calculated E , the distance between the trajectory based on the whole community (ALL) and the trajectory based on each of the data sets excluding groups of species (e.g., ALL vs $ALL_{w/o SSM}$; ALL vs $ALL_{w/o LSM}$). E was calculated as: $E_{jk} = \sum_{i=1}^N \frac{S_{ij} - S_{ijk}}{N-1}$, where S_{ij} is the observed taxonomic similarity for all species in the plot j and the interval i , S_{ijk} is the observed taxonomic similarity for the data set excluding the group of species k in the plot j and the interval i and N is the number of time intervals of each pairwise trajectory. By doing this, we obtained distinct E values that resulted from the comparison between trajectories in temporal turnover values for the whole community and turnover values for subsets of species that excluded species based on seed size and wood density values (Figure 1).

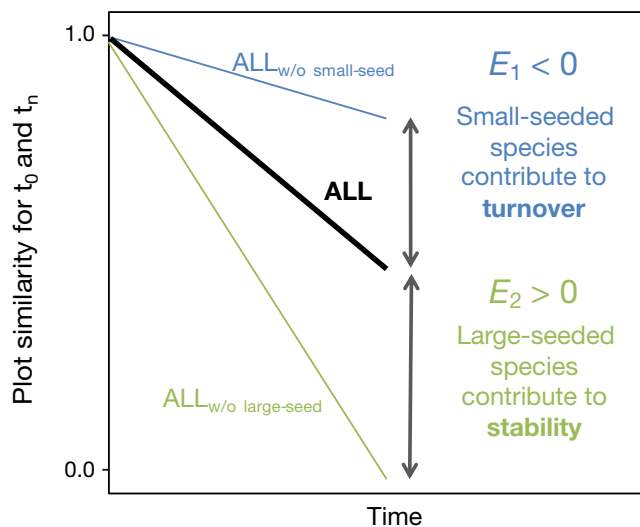


FIGURE 1 Conceptual diagram depicting the contribution of small- and large-seeded species to temporal taxonomic turnover in tree communities. The black line (ALL) represents the trajectory of taxonomic similarity over time for the whole community in a given plot. The blue line ($ALL_{w/o SSM}$) depicts the trajectory when species with small seeds were removed from the community, and the green line ($ALL_{w/o LSM}$) depicts the trajectory when species with large seeds were removed. E represents the distance between the trajectory with all species (ALL, black line) and the blue or green trajectories. If $E < 0$ the group of species that was removed (blue line), in this case, the small-seeded species, contributes to taxonomic turnover. If $E > 0$ the group of species that was removed contributes to maintaining taxonomic similarity over time (green line)

To interpret results in terms of species contribution to temporal turnover (e.g., species showing fast turnover or more stable dynamics), and to make them comparable across similarity indices, we normalized E by dividing its value by the maximum number of intervals examined for that given subplot. Positive E values indicate that the removal of a specific group of species results in a decrease in temporal taxonomic similarity so that these species contribute to stability over time. Conversely, negative E values indicate that removing a specific group of species results in an increase in temporal taxonomic similarity, implying that these species contribute to taxonomic turnover over time (Figure 1). Finally, we performed a non-parametric Kruskal–Wallis and Dunn's post-hoc analyses to test for significant differences in E across the different seed size/wood density groups.

Because removing subsets of species leads to changes in alpha diversity within plots, we evaluated the correlation between our response variable E and species richness and abundance per plot to determine whether our results were driven by either species richness or tree abundance. We found no relationship between species richness or abundance and E which indicates that variation in species richness/abundance is not driving our results. All supplementary results are presented in Appendix S2. We also used a null model approach to account for a potential spurious effect of removing species across bins (Chase et al., 2011). To do so, we randomized species labels in the trait matrix 999 times. We performed all the analyses described above to obtain 999 null chi-squared values from the Kruskal–Wallis test. Next, we compared the null chi-squared values with the observed chi-squared value by examining where the observed value ranks in the null distribution. If the quantile of observed chi-squared values were ≥ 0.975 or ≤ 0.025 , the differences were considered significant. The specific methods for the null model implementation are described in Appendix S3.

Our analyses were based on comparisons using the year 2001 as the starting point (Appendix S1). We repeated the analyses using the year 2002 as the starting point to examine whether the use of different starting censuses (t_0) leads to varying patterns of taxonomic turnover (Appendix S1). Given that the set of plots censused in 2001 and 2002 do not completely overlap, this new analysis resulted in the evaluation of temporal species turnover for 1651 plots instead of 1053. Since variation in taxonomic similarity was largely consistent for both sets of analyses (Appendix S1), we present results using the year 2001 as the starting point.

Finally, to assess how demographic rates of species with distinct seed size and wood density values explain differences in the temporal turnover observed, we evaluated the extent to which differences across species in tree recruitment rates (new individuals with DBH > 12.7 cm entering the community) and/or survival contributed to community dynamism or stability over time. To do so, we compared recruits and survivors in each census interval for each of the seed mass and wood density groups, using *bin-3* and *bin-2*, quantified as a proportion of total subplot stem density. We then used Kruskal–Wallis and post-hoc Dunn's tests to test for significant differences in median recruitments and survival across the seed mass and wood density groups. All analyses were performed in R 3.4.0 (R Development Core Team).

3 | RESULTS

3.1 | Differences in species contribution to taxonomic turnover among seed mass groups

We found a progressive decline in taxonomic similarity over time across all three indices (Sørensen, Horn, and Morisita–Horn), indicating that tree communities tend to diverge from the starting species composition (Appendix S1). This trend was the result of different groups of species showing contrasting contributions to the forest dynamics. Specifically, depending on seed mass, species showed different contributions to community dynamism and stability over time (Figure 2, Appendix S2). Based on the *bin-3* classification and all three metrics (Sørensen, Horn, and Morisita–Horn), small-seeded species contributed the most to community dynamism (e.g., decreasing similarity), followed by medium, and finally by large-seeded species (Figure 2, Appendix S1). These observations were also supported by results from the null model approach (Appendix S3). Based on the *bin-2* classification, we found no significant differences in the contribution to taxonomic turnover of large- and small-seeded species (Appendix S1).

3.2 | Differences in species contribution to taxonomic turnover among wood density groups

Wood density was also related to the way species contribute to patterns of community dynamism and stability over time (Figure 3, Appendix S1). Based on the *bin-3* classification, low wood density species contributed the most to community dynamism compared to medium and high wood density species for Horn and Morisita–Horn indices (Figure 3, Appendix S1). Also, medium wood density

species contributed significantly more to community dynamism than high wood density species for all three indices (Appendix S1). These results were also supported by results obtained using the null model approach (Appendix S3). When using the *bin-2* classification, we found that low wood density species contributed more to community dynamism than high wood density species (Appendix S1). The null models did not support these results (Appendix S3).

3.3 | Differences in recruitment and survival across seed mass and wood density groups

The proportion of newly recruited individuals and of survivors was significantly different among species groups depending upon seed mass and wood density. For *bin-3*, small-seeded species exhibited a lower proportion of recruits and survivors than medium- and large-seeded species (Figure 4). Also, medium wood density species showed a significantly lower proportion of recruits, followed by low wood density species and then by high wood density species. Medium and low wood density species exhibited a significantly lower proportion of survivors than high wood density species (Figure 4). For *bin-2*, small-seeded species exhibited a significantly lower proportion of recruits and survivors than large-seeded species, but we did not find significant differences for analyses based on wood density groups (Appendix S1).

4 | DISCUSSION

By examining patterns of temporal turnover in taxonomic composition over a period of 14 years in northeastern American forests,

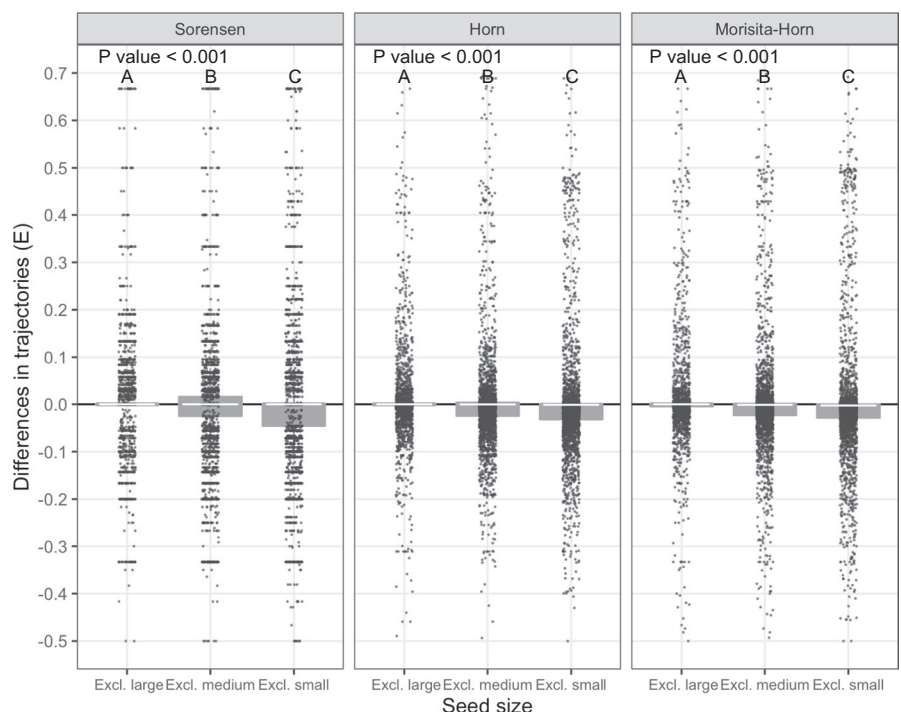


FIGURE 2 Boxplot showing differences in the distance, *E*, between trajectories that included all species (ALL) and those that excluded species based on differences in seed mass (ALL_{w/o LSM}, excl. large; ALL_{w/o MSM}, excl. medium; ALL_{w/o SSM}, excl. small seed mass). Positive *E* values indicate that excluded species contribute to community stability over time. Negative *E* values indicate that excluded species contribute to community dynamism. Letters indicate the significant differences among groups. The white horizontal line in the boxes indicates the median and the boxes' lower and upper limits represent the 25th and 75th quantiles respectively

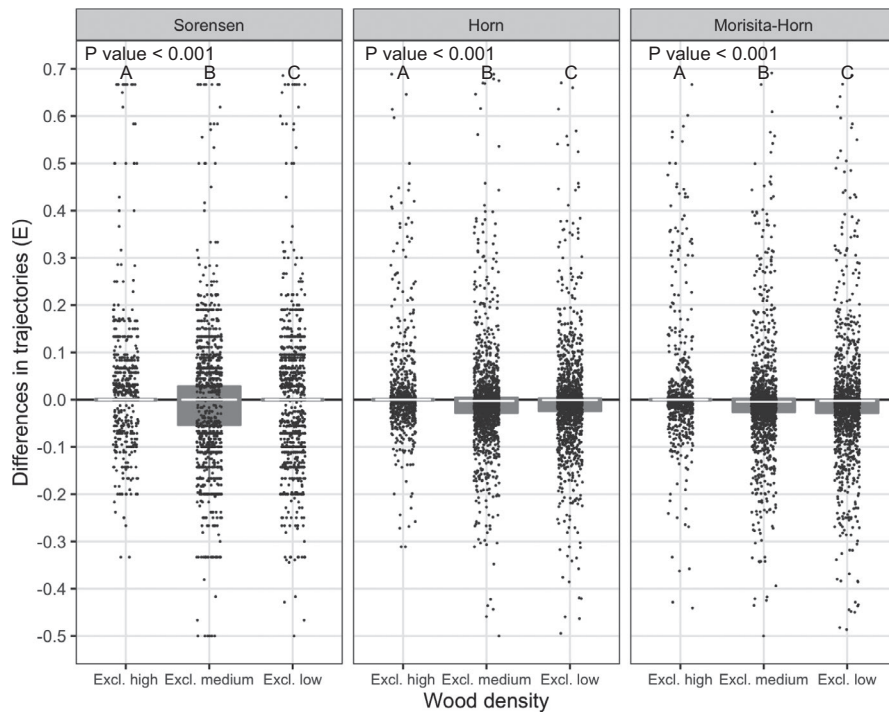


FIGURE 3 Boxplot showing differences in the distance, E , between trajectories that included all species (ALL) and those that excluded species based on differences in wood density (ALL_{w/o HWD}, ALL_{w/o MWD}, ALL_{w/o LWD} without high, medium, or low wood density species, respectively). Positive E values indicate that excluded species contribute to community stability over time. Negative E values indicate that excluded species contribute to community dynamism. Letters indicate the significant differences among groups. The white horizontal line in the boxes indicates the median and the boxes' lower and upper limits represent the 25th and 75th quantiles respectively

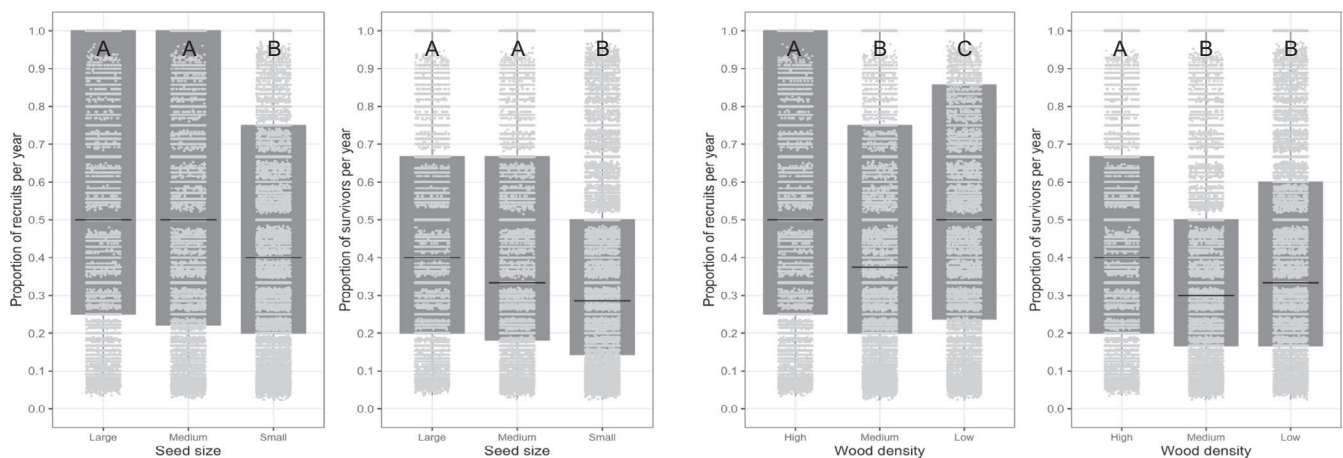


FIGURE 4 Differences in proportion of tree recruits (new individuals with DBH > 12.7 cm entering the community) and survivors per plot per census across groups of different seed masses and wood densities (*bin-3*). The different letters indicate significant differences ($\alpha = 0.05$, Kruskal-Wallis test)

we showed that forest dynamics are the outcome of the opposing contributions of groups of species with distinct seed mass and wood density that simultaneously promote either stability or dynamism. Specifically, small-seeded and low wood density species contributed the most to dynamism over time compared to large-seeded and high wood density species. These trends were related to the combination of low tree survival and low replacement of small-seeded species, as well as low tree survival of low wood density species.

4.1 | Small-seeded species are major drivers of community dynamism

Changes in taxonomic composition over time in tree communities are the result of demographic processes, which in turn depend on

species' functional traits. We expected that small-seeded species would contribute more to community dynamism than large-seeded species as they have greater colonization abilities and shorter life spans, and are thereby likely to exhibit higher recruitment but low survival rates (Harper et al., 1970; Howe & Westley, 1986; Muller-Landau, 2010; Venable & Brown, 1988). Our findings partially support this hypothesis, as small-seeded species did show a higher contribution to turnover through low survival, yet they also exhibited low recruitment rates into the adult stage (individuals reaching a DBH > 12.7 cm). This might be explained by the fact that although small-seeded species are expected to exhibit high recruitment rates at the seedling stage, here, we are evaluating recruitment to later stages. Thus, the low recruitment observed is likely the result of low survival rates in earlier stages that prevent the recruitment of individuals at the stage studied here. Due to low tree survival and low

replacement rates, small-seeded species are disappearing faster than large-seeded species from plant communities, promoting changes in species' relative abundance. Examples of species with small seed mass in our data set include some *Betula* species, which are typically short-lived and common after disturbance, suggesting that forests in this region may be reaching advanced stages of succession (Smith & Ashton, 1993). However, other less light-demanding species, which are indeed common components of old-growth forests, such as *Abies balsamea*, also have small seeds. Since populations of *Abies balsamea* are often severely impacted by wind disturbance in mountain regions (Sprugel, 1976), the fast dynamics displayed by small-seeded species may be associated with different drivers – wind disturbance eliminating old-growth species or advanced succession promoting the disappearance of pioneer species. Surprisingly, results based on the *bin-2* classification did not show significant differences between small- and large-seeded species in their contribution to temporal turnover. A potential explanation for this result is that the *bin-2* classification divided species into two groups that were highly heterogeneous (e.g., the range of seed mass values varied by two orders of magnitude for the small-seeded group and by three orders of magnitude in the large-seeded group). This high heterogeneity within groups may have obscured the trends across groups.

4.2 | Low wood density species are major drivers of community dynamism

Similar to small-seeded species, and in agreement with our predictions, low wood density species contributed the most to forest dynamism. This group included species of the genus *Populus*, common in regenerating gaps and in successional forests of the northeastern American stands (Foster, 1992; Thompson et al., 2013). *Populus* species exhibit acquisitive strategies, characterized by fast growth rates enabling them to take advantage of high light conditions at the expense of longevity. As expected, low wood density species experienced lower survival than high wood density species, thereby contributing to community turnover over time. These findings support previous studies indicating that forest stands of the northeastern United States are undergoing succession, where early and mid-successional species, often characterized by low wood density, short life cycles, and low self-replacement rates, are being replaced by old-growth forest species (Foster et al., 1998). However, other non-exclusive drivers of fast dynamics include climate change, responsible for increases in the intensity of drought events, causing recent die-offs of *Populus* species (Anderegg et al., 2012). Likewise, *Abies balsamea* fell within the low wood density group and it is likely associated with the wind-driven regeneration dynamics (Sprugel, 1976). Our results suggest that community dynamism is likely promoted by a combination of factors where successional changes are not the only driver of fast turnover rates.

These forests also harbor less dynamic species with higher wood density and low turnover rates. Some of these species are

represented by relicts restricted to specific regions within the United States (Thompson et al., 2013). This is the case of the American chestnut (*Castanea dentata*), which experienced an important historical decline in its population due to a pathogenic fungus during the late 1930s and, in the present, the population size of this species remains small (Ellison et al., 2005; Paillet, 2002). Other species within the more stable dynamics groups are represented by old-growth forest species (e.g., beech [*Fagus*]).

Here, we propose to characterize fast-dynamic species as transient components of communities while the core species would be those that rather contribute to stability. The classification of communities into core and transient species has a long history in ecology and has often been associated with species abundance, where rare species tend to be at higher risk of extinction and therefore are less persistent in the communities (Hanski, 1982; Magurran & Henderson, 2003). However, our results show that the contribution to fast or stable dynamics is not necessarily linked to species abundance, as shown by the consistency in trends observed across the different metrics examined that include incidence- and abundance-based indices. We also examined the relationship between species traits and species abundance, but the relationship was not significant (Appendix S1), which also suggests that species abundance is not driving the patterns observed. Thus, classification of species as core or transient is complicated and does not necessarily correspond to the variation in species abundance (Coyle et al., 2013).

4.3 | Potential contributing factors to northeastern American temperate forest dynamics

Although we detected significant differences in the contribution to taxonomic turnover across groups of species with differing seed mass and wood density, the results also show important variation in the contribution of the species within each of the groups. Such a variation is expected as the data set is highly heterogeneous and represents a large area. Indeed, the observed dynamics are likely the product of multiple contributing factors including diseases, natural and anthropogenic disturbance, and climate change (Abrams & Nowacki, 1992; Bürgi et al., 2000; Coble et al., 2017; Nowacki & Abrams, 1992; Wang et al., 2009). For instance, the average summer temperatures in the northeastern United States has been increasing by 0.1°C per decade and, in the long term, these changes may result in shifts in forest composition and dynamics (Rustad et al., 2012). We therefore examined the effect of precipitation and temperature on temporal turnover over the 14-year period, yet our results showed non- or weakly significant trends (see Appendix S4), suggesting that trends detected in our study are not likely to be explained by climatic changes. Temperature changes so far may not be strong enough to impact shifts in tree species composition for the 14-year period studied here. Considering that trees are long-lived organisms, longer-term data are necessary to thoroughly evaluate the effects of climate change on forest community dynamics.

5 | CONCLUSION

We show that forest dynamics can be partially explained by a differential contribution of species with contrasting seed and wood traits that simultaneously promote stability and dynamism. Specifically, we found that fast taxonomic turnover in temperate forests is promoted by the presence of small-seeded and low wood density species, while species with more conservative ecological strategies characterized by high survival rates tended to contribute more to stability. These results further highlight the fact that forest dynamics rather than being considered as a homogenous and coordinated change of species over time reflect more individualistic contributions of groups of species. By accounting for species demography and traits, we can better disentangle species contribution to temporal turnover patterns, especially in areas that have undergone a complex history of disturbance, diseases, and climatic changes such as the northeastern United States forests.

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AUTHOR CONTRIBUTIONS

María Natalia Umaña and Natalia Norden conceived the conceptual framework. María Natalia Umaña and Natalia Norden designed the analyses, María Natalia Umaña conducted the analyses, Jenny Zambrano prepared the FIA data for analysis. María Natalia Umaña wrote the first draft and all authors contribute significantly to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

The trait information is provided in the supplemental material. The census information is stored in Dryad (<http://dx.doi.org/10.5061/dryad.pv8s1>).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Supplementary results

Appendix S2. Relationship between species richness, abundance and *E* values

Appendix S3. Analyses including temperature and precipitation

Appendix S4. Null models

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