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Research Article

Short running title: Temporal turnover and tree traits

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

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29 distinct subsets of species. Specifically, fast taxonomic turnover should be promoted by
30 species that take advantage of sporadically available resources, while forest stability
31 should be promoted by species with conservative and stress-tolerant life-histories.

- 32 • Location: Northeastern USA.
- 33 • Methods: We combine demographic information (survival, recruitment) over a 14-yr
34 period from temperate tree communities in the northeastern USA with trait information
35 on species seed mass and wood density as a proxy for their reproductive and resource
36 acquisition strategies, to evaluate the differential contribution of species with contrasting
37 ecological strategies (low vs. high seed mass/wood density) to rates of compositional
38 turnover in temperate forests.
- 39 • Results: The apparent dynamism of USA forests is mostly driven by high mortality and
40 low recruitment of small-seeded species and by high mortality and recruitment of low
41 wood density species. Simultaneously, species with the opposite traits, i.e., high seed
42 mass and wood density, contribute more to stability. Our findings suggest that forests
43 dynamics in the northeastern USA are the outcome of opposing contributions of life
44 history and plant traits that simultaneously promote forest stability and rapid taxonomic
45 turnover by operating differentially across tree species.
- 46 • Conclusions: Small-seeded and low wood density species promote faster forest turnover
47 than species with the opposite traits. Not accounting for these functional differences in
48 community-level analyses is likely to mask the complex dynamics of temperate forests.
49 This study demonstrates the importance of studying forest composition and structure
50 under a dynamic scope that accounts for differences in functional strategies across
51 species.

52 **Keywords:** community diversity, community dynamics, seed mass, temporal turnover,
53 temperate tree communities, wood density.

54 **Introduction**

55 Understanding plant community dynamics –shifts in taxonomic and functional composition over
56 time– is needed for predicting forest changes, a critical matter under current and projected
57 climatic scenarios (Parmesan & Yohe 2003). Addressing this issue, however, is particularly
58 challenging because multiple drivers, including climate, pests, and disturbance, simultaneously
59 operate on forest communities and may have opposing effects on floristic composition. For

60 instance, a recent study in the forests of North America suggests that changes in climate are
61 favoring drought-tolerant over drought-intolerant species (Trugman et al. 2020), yet successional
62 processes in these same forests are simultaneously benefiting the establishment of early/mid
63 successional species, which tend to underperform in conditions of low water availability
64 (Chapman & McEwan 2016). Similarly, while climatic conditions might favor the establishment
65 of species able to cope with new stresses, species-specific pests might heavily impair the
66 performance of some of these species (Abrams and Mostoller 1995). These conflicting responses
67 may nullify each other resulting in a net outcome that does not reveal all the complexity of
68 processes driving forest dynamics, and thereby imposing important challenges for predicting the
69 fate of today's forests. For temperate forests in the USA, it is well known that species may
70 respond idiosyncratically to different factors (Sprugel 1976; Davis & Woods 1989; McEwan et
71 al. 2011). Reaching a synthetic understanding of shifts in community composition requires
72 moving beyond the notion that plant dynamics are an aggregated and coordinated change in
73 species composition over time towards a more individualistic view of dynamics where species
74 have different contributions to temporal turnover (Gleason 1926).

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

91 To gain further insight into the complexity of forests' community-level temporal
92 taxonomic turnover, we propose to identify the relative contribution of different tree species to
93 forest dynamics, depending upon their functional traits –morphological and physiological
94 attributes that influence the interaction between an organism and its surrounding environment
95 (Arnold 1983; McGill et al. 2006; Violle et al. 2007). Seed size and wood density show
96 important variation across species (Westoby 1998; Díaz et al. 2016) and are critical traits
97 determining plant demography and ultimately forest dynamics (Chave et al. 2009; Adler et al.
98 2014). In particular, seed mass represents a trade-off between producing many small, stress-
99 intolerant seeds or few large, stress-tolerant seeds (Muller-Landau, 2010; Rees, 1995; Turnbull,
100 Rees, & Crawley, 1999; Westoby, Jurado, & Leishman, 1992). Small-seeded species are
101 recognized to have good colonization abilities as they can disperse widely and have high
102 potential rates of per capita seedling recruitment, but may fail to persist in older size classes due
103 to their low stress-tolerance (Coomes & Grubb, 2003; Everham III, Myster & VanDeGenachte,
104 1996; but see Moles, 2018). In contrast, large-seeded species are stress-tolerant, which in turn
105 leads to high survival rates yet accompanied by low seedling recruitment due to low per capita
106 seed production (Muller-Landau 2010). Similarly, variation in wood density reflects differences
107 in a range of ecological strategies in which high wood density species tend to have long life-
108 spans and conservative resource-use strategies, while low wood density species typically exhibit
109 short life cycles and are characterized by acquisitive resource-use strategies (Wright et al. 2010;
110 Osazuwa-Peters et al. 2017). In brief, small-seeded and/or low wood density species, associated
111 with fast demography (either low survival or high seedling recruitment), are expected to
112 contribute to rapid turnover in taxonomic composition over time, while large-seeded and/or high
113 wood density species, which exhibit slow demography, are expected to contribute to taxonomic
114 stability.

115 In this study, we evaluated the role of traits promoting either dynamism or stability in tree
116 species in temperate forests. We examined patterns of tree species turnover across 1053 forest
117 plots monitored over a 14-yr period in the Northeast USA. The forests in this region are at
118 different successional stages and are currently undergoing shifts in species composition and
119 dominance due to variable disturbance history, abiotic factors, climatic factors, and diseases
120 (Abrams & Nowacki 1992; Bürgi et al. 2000; Thompson et al. 2013). We hypothesized that
121 small-seeded and low wood density species contribute to rapid changes in community

122 composition over time, while large-seeded and low wood density species contribute to
123 taxonomic stability. These patterns should be the result of different demographic processes
124 where taxonomic turnover driven by small-seeded species and low wood density species may
125 occur through high recruitment and/or low survival of these species. Specifically, we asked: (1)
126 What is the contribution of species with different seed sizes and wood densities to patterns of
127 turnover in community composition? (2) How do demographic rates (i.e., recruitment and
128 survival) of species with distinct seed size and wood density values explain differences in
129 temporal turnover at the community level?

130

131 **Materials and methods:**

132 Survey data: We used data from the northeast USA Forest Inventory and Analyses database
133 (FIA) that included local tree communities across 13 states (Connecticut, Delaware, Maine,
134 Maryland, Massachusetts, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode
135 Island, Vermont, and West Virginia). We selected communities monitored from 2001 to 2014
136 across 1053 permanent plots (three census periods per plot) and including 25 tree species. Each
137 plot consisted of four circular subplots with a 7.32 m fixed radius and separated by 36.6 m.
138 Within each plot, all trees with a diameter at breast height (DBH) > 12.7cm were tagged,
139 identified, and monitored for survival. We used subplots as our sampling unit for all the analyses.
140 We included plots that fulfill following conditions: 1) plots measured at least twice, 2) no
141 evidence of logging since the last measurement, 3) no evidence of damage by insects, disease or
142 fire since the last measurement, and 4) closed-canopy forests that included plots established in
143 forested land (with at least 10% cover by live trees of any size). Agriculturally managed areas
144 such as fruit orchards, or land areas in urban sites such as city parks were not considered in this
145 study (Woudenberg et al. 2010). The selected plots represented closed-canopy forests in the
146 Northeast US that have not been disturbed in the recent past (2000-2014) but could have been
147 disturbed before the studied period representing secondary forests.

148 Trait data: We compiled information on seed mass (mg) and wood density ($\text{g}\cdot\text{cm}^{-3}$) from the
149 Seed Information Database (SID) from the Kew Royal Botanic Gardens webpage
150 (<http://data.kew.org/sid/>) and the Global wood density Database webpage
151 (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.234>), respectively. Both traits were

152 moderately correlated ($r = 0.5$, $P = 0.02$, Appendix S1, Fig. S1.1) and were not related to species
153 abundance (Appendix S1, Fig. S1.2-3).

154

155 Analyses: We evaluated changes in taxonomic similarity for each subplot over 14 years
156 (temporal turnover) by calculating similarity in species composition between consecutive
157 censuses based on Hill numbers using as a reference point the species composition in the first
158 census. This way, we obtained a trajectory for each plot composed of two similarity values. Hill
159 numbers represent the effective number of species, in other words, the number of equally
160 abundant species needed to get the same diversity value (Chao, Chiu, et al. 2014). Although Hill
161 numbers have been typically used to evaluate alpha-diversity, they can also serve to measure
162 taxonomic similarity. Specifically, to compare pairs of assemblages (e.g. *subplot_i* at census 1 and
163 *subplot_i* at census 2), Hill numbers of the pooled assemblages (gamma diversity) were
164 decomposed into independent alpha and beta components of diversity and monotonically
165 transformed into similarity measures (Chao, Chiu, et al. 2014). These indices are more
166 appropriate than other commonly used metrics because they obey to the replication principle
167 (linearity with respect to increases in diversity) (Jost 2006; Jost et al. 2011; Chao, Gotelli, et al.
168 2014). We used three similarity metrics that differentially weight species abundance (number of
169 individuals). The incidence-based Sørensen index, and the abundance-based, Horn and Morisita-
170 Horn indices, give values for subplot floristic similarity between time t_0 and time t_n , where n
171 represents the year when a specific tree community was re-censused (Chao, Chiu, et al. 2014).
172 We selected t_0 as the reference point to be able to compare changes in taxonomic similarity over
173 time. The Sørensen index weighs all species equally, while the Horn index weighs each species
174 based on their relative abundance (Horn 1966; Jost et al. 2011). The Morisita-Horn is more
175 sensitive to dominant species, while the Horn index is more susceptible to the abundance of rare
176 species (Jost et al. 2011).

177 To examine the contribution of species seed mass and wood density to taxonomic
178 turnover over time, we performed a sensitivity analysis evaluating the effect of removing subsets
179 of species depending on their morphological traits in temporal species turnover, following
180 Norden *et al.* (2017). To do so, we first classified all species using bins (Appendix S1, Tables
181 S1.1 & S1.2). *bin-2* separated species into two categories by keeping a similar number of species
182 in each category (small- and large-seeded species: 12 and 13 species respectively; high and low

183 wood density species: 12 and 13 species respectively; Table S1.1). *bin-3* separated seed mass
184 into three categories (small, medium and large) based on differences in orders of magnitude
185 (small: 0 to <10 mg (9 species), medium: 10 to <100 mg (9 species) and large: ≥ 100 mg (7
186 species); Table S1.1). For wood density, given that the total range of variation in this trait did not
187 cover several orders of magnitude as for seed mass, the *bin-3* classification was performed to
188 keep a similar number of species in each of the three categories (low wood density: 7 species,
189 medium wood density: 8 species, high wood density: 9 species; Table S1.2). Once these classes
190 were defined, we recalculated, for each subplot, taxonomic similarity between t_0 and t_n over the
191 14 years following removal of each of these groups of species, one at a time (e.g., $ALL_{w/o LSM}$ =
192 excludes species with large seed mass; $ALL_{w/o MSM}$ = excludes species with medium seed mass;
193 $ALL_{w/o SSM}$ = excludes species with small seed mass) and obtained a new trajectory of similarity
194 values over the studied time period (14 years) for each dataset.

195 We then compared temporal turnover, as measured in similarity values between
196 consecutive censuses, for the whole community (that is, including all species within each
197 subplot: ALL) to patterns obtained when removing subsets of species belonging to groups
198 characterized by their seed size and wood density, separately. For example, for each subplot, we
199 compared the trajectory describing temporal turnover based on the whole-community (ALL) to
200 that obtained when removing large-seeded species ($ALL_{w/o LSM}$) (Fig. 1). We then repeated this
201 procedure for all the categories of the two bins (e.g., for *bin-2* & seed mass: ALL vs. $ALL_{w/o LSM}$,
202 ALL vs. $ALL_{w/o SSM}$; for *bin-2* & wood density: ALL vs. $ALL_{w/o LDW}$, ALL vs. $ALL_{w/o HWD}$).
203 Next, we calculated E , the distance between the trajectory based on the whole-community (ALL)
204 and the trajectory based on each of the datasets excluding groups of species (e.g., ALL vs.
205 $ALL_{w/o SSM}$; 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
206 observed taxonomic similarity for all species in the plot j and the interval i , S_{ijk} is the observed
207 taxonomic similarity for the dataset excluding the group of species k in the plot j and the interval
208 i and N is the number of time intervals of each pairwise trajectory. By doing this, we obtained
209 distinct E values that resulted from the comparison between trajectories in temporal turnover
210 values for the whole community and turnover values for subsets of species that excluded species
211 based on seed size and wood density values (Fig. 1).

212 To interpret results in terms of species contribution to temporal turnover (e.g., species
213 showing fast turnover or more stable dynamics), and to make them comparable across similarity

214 indices, we normalized E by dividing its value by the maximum number of intervals examined
215 for that given subplot. Positive E values indicate that the removal of a specific group of species
216 results in a decrease in temporal taxonomic similarity so that these species contribute to stability
217 over time. Conversely, negative E values indicate that removing a specific group of species
218 results in an increase in temporal taxonomic similarity implying that these species contribute to
219 taxonomic turnover over time (Fig. 1). Finally, we performed a non-parametric Kruskal-Wallis
220 and Dunn's post-hoc analyses to test for significant differences in E across the different seed
221 size/wood density groups.

222 Because removing subsets of species leads to changes in alpha diversity within plots, we
223 evaluated the correlation between our response variable E and species richness and abundance
224 per plot to determine whether our results were driven by either species richness or tree
225 abundance. We found no relationship between species richness or abundance and E which
226 indicates that variation in species richness/abundance is not driving our results. All
227 supplementary results are presented in Appendix S2 (Figs. S2.1-S2.4). We also used a null model
228 approach to account for a potential spurious effect of removing species across bins (Chase et al.
229 2011). To do so, we randomized species labels in the trait matrix 999 times. We performed all the
230 analyses described above to obtain 999 null Chi^2 values from the Kruskal-Wallis test. Next, we
231 compared the null Chi^2 values with the observed Chi^2 value by examining where the observed
232 value ranks in the null distribution. If the quantile of observed Chi^2 values were ≥ 0.975 or
233 ≤ 0.025 , the differences were considered significant. The specific methods for the null model
234 implementation are described in Appendix 3.

235 Our analyses were based on comparisons using the year 2001 as the starting point (Fig.
236 S1.4). We repeated the analyses using the year 2002 as the starting point to examine whether the
237 use of different starting censuses (t_0) leads to varying patterns of taxonomic turnover (Fig. S1.5).
238 Given that the set of plots censused in 2001 and 2002 do not completely overlap, this new
239 analysis resulted in the evaluation of temporal species turnover for 1651 plots instead of 1053.
240 Since variation in taxonomic similarity was largely consistent for both sets of analyses (Fig.
241 S1.5, Table S1.3), we present results using the year 2001 as the starting point.

242 Finally, to assess how demographic rates of species with distinct seed size and wood
243 density values explain differences in the temporal turnover observed, we evaluated the extent to
244 which differences across species in tree recruitment rates (new individuals with more DBH >

245 12.7 cm entering the community) and/or survival contributed to community dynamism or
246 stability over time. To do so, we compared recruits and survivors in each census interval for each
247 of the seed mass and wood density groups, using *bin-3* and *bin-2*, quantified as a proportion of
248 total subplot stem density. We then used Kruskal-Wallis and post-hoc Dunn's tests to test for
249 significant differences in median recruitments and survival across the seed mass and wood
250 density groups. All analyses were performed in R 3.4.0 (R Development Core Team 2017).

251

252 **Results**

253 *Differences in species contribution to taxonomic turnover among seed mass groups*

254 We found a progressive decline in taxonomic similarity over time across all three indices
255 (Sørensen, Horn, and Morisita-Horn), indicating that tree communities tend to diverge from the
256 starting species composition (Fig. S1.4). This trend was the result of different groups of species
257 showing contrasting contributions to the forest dynamics. Specifically, depending on seed mass,
258 species showed different contributions to community dynamism and stability over time (Fig. 2,
259 Table S1.3). Based on the *bin-3* classification and all three metrics (Sørensen, Horn, and
260 Morisita-Horn), small-seeded species contributed the most to community dynamism (e.g.,
261 decreasing similarity), followed by medium, and finally by large-seeded species (Fig. 2, Table
262 A1.3). These observations were also supported by results from the null model approach
263 (Appendix S3, Fig. S3.1). Based on the *bin-2* classification, we found no significant differences
264 in the contribution to taxonomic turnover of large- and small-seeded species (Fig. S1.6, Table
265 A1.3).

266

267 *Differences in species contribution to taxonomic turnover among wood density groups*

268 Wood density was also related to the way species contribute to patterns of community dynamism
269 and stability over time (Fig. 3, Table S1.3). Based on the *bin-3* classification, low wood density
270 species contributed the most to community dynamism compared to medium and high wood
271 density species for Horn and Morisita-Horn indices (Fig. 3, Table S1.3). Also, medium wood
272 density species contributed significantly more to community dynamism than high wood density
273 species for all three indices (Table S1.3). These results were also supported by results obtained
274 using the null model approach (Appendix S3 Fig. S3.2). When using the *bin-2* classification, we

275 found that low wood density species contributed more to community dynamism than high wood
276 density species (Fig. S1.7, Table S1.3). The null models did not support these results.

277

278 *Differences in recruitment and survival across seed mass and wood density groups*

279 The proportion of newly recruited individuals and of survivors was significantly different among
280 species groups depending upon seed mass and wood density. For *bin-3*, small-seeded species
281 exhibited a lower proportion of recruits and survivors than medium- and large-seeded species
282 (Fig. 4). Also, medium wood density species showed a significantly lower proportion of recruits,
283 followed by low wood density species and then by high wood density species. Medium and low
284 wood density species exhibited a significantly lower proportion of survivors than high wood
285 density species (Fig. 4). For *bin-2*, small-seeded species exhibited a significantly lower
286 proportion of recruits and survivors than and large-seeded species, but we did not find significant
287 differences for analyses based on wood density groups (Fig. S1.8).

288

289 **Discussion**

290 By examining patterns of temporal turnover in taxonomic composition over a period of 14 years
291 in northeastern USA forests, we showed that forest dynamics are the outcome of the opposing
292 contributions of groups of species with distinct seed mass and wood density that simultaneously
293 promote either stability or dynamism. Specifically, small-seeded and low wood density species
294 contributed the most to dynamism over time compared to large-seeded and high wood density
295 species. These trends were related to the combination of low tree survival and low replacement
296 of small-seeded species, as well as low tree survival of low wood density species.

297

298 *Small-seeded species are major drivers of community dynamism*

299 Changes in taxonomic composition over time in tree communities are the result of demographic
300 processes, which in turn depend on species' functional traits. We expected that small-seeded
301 species would contribute more to community dynamism than large-seeded species as they have
302 greater colonization abilities and shorter life-spans, and are thereby likely to exhibit higher
303 recruitment but low survival rates (Harper et al. 1970; Howe & Westley 1986; Venable & Brown
304 1988; Muller-Landau 2010). Our findings partially support this hypothesis, as small-seeded
305 species did show higher contribution to turnover through low survival, yet they also exhibited

306 low recruitment rates into the adult stage (individuals reaching a DBH > 12.7 cm). This might be
307 explained by the fact that although small-seeded species are expected to exhibit high recruitment
308 rates at the seedling stage, here we are evaluating recruitment to latter stages. Thus, the low
309 recruitment observed is likely the result of low survival rates in earlier stages that prevent the
310 recruitment of individuals at the stage studied here. Due to low tree survival and low replacement
311 rates, small-seeded species are disappearing faster than large-seeded species from plant
312 communities, promoting changes in species relative abundance. Examples of species with small
313 seed mass in our dataset include some *Betula* species, which are typically short-lived and
314 common after disturbance, suggesting that forests in this region may be reaching advanced stages
315 of succession (Smith & Ashton 1993). However, other less light-demanding species, which are
316 indeed common components of old-growth forests, such as *Abies balsamea*, also have small
317 seeds. Since populations of *A. balsamea* are often severely impacted by wind disturbance in
318 mountain regions (Sprugel, 1976), the fast dynamics displayed by small-seeded species may be
319 associated with different drivers –wind disturbance eliminating old-growth species or advanced
320 succession promoting the disappearance of pioneer species. Surprisingly, results based on the
321 *bin-2* classification did not show significant differences between small- and large-seeded species
322 in their contribution to temporal turnover. A potential explanation for this result is that the *bin-2*
323 classification divided species into two groups that were highly heterogeneous (e.g., the range of
324 seed mass values varied by two orders of magnitude for the small-seeded group and by three
325 orders of magnitude in the large-seeded group). This high heterogeneity within groups may have
326 obscured the trends across groups.

327

328 *Low wood density species are major drivers of community dynamism*

329 Similar to small-seeded species, and in agreement with our predictions, low wood density
330 species contributed the most to forest dynamism. This group included species of the genus
331 *Populus*, common in regenerating gaps and in successional forests of the northeast USA stands
332 (Foster, 1992; Thompson *et al.*, 2013). *Populus* species exhibit acquisitive strategies,
333 characterized by fast growth rates enabling them to take advantage of high light conditions at the
334 expense of longevity. As expected, low wood density species experienced lower survival than
335 high wood density species, thereby contributing to community turnover over time. These
336 findings support previous studies indicating that forest stands of Northeastern USA are

337 undergoing succession, where early and mid-successional species, often characterized by low-
338 wood density, short life cycles, and low self-replacement rates, are being replaced by old-growth
339 forest species (Foster *et al.*, 1998). However, other non-exclusive drivers of fast dynamics
340 include climate change, responsible for increases in the intensity of drought events, causing
341 recent die-offs of *Populus* species (Anderegg *et al.* 2012). Likewise, *A. balsamea* fell within the
342 low-wood density group and it is likely associated with the wind-driven regeneration dynamics
343 (Sprugel 1976). Our results suggest that community dynamism is likely promoted by a
344 combination of factors where successional changes are not the only driver of fast turnover rates.

345 These forests also harbor less dynamic species with higher wood density and low
346 turnover rates. Some of these species are represented by relicts restricted to specific regions
347 within the USA (Thompson *et al.* 2013). This is the case of the American chestnut (*Castanea*
348 *dentata*), which experienced an important historical decline in its population due to a pathogenic
349 fungus during the late-1930s and, in the present, the population size of this species remains small
350 (Paillet 2002; Ellison *et al.* 2005). Other species within the more stable dynamics groups are
351 represented by old-growth forest species (e.g., beech-*Fagus*).

352 Here, we propose to characterize fast-dynamic species as transient components of
353 communities while the core species would be those that rather contribute to stability. The
354 classification of communities into core and transient species has a long history in ecology and
355 has been often associated with species abundance, where rare species tend to be at higher risk of
356 extinction and therefore are less persistent in the communities (Hanski 1982; Magurran &
357 Henderson 2003). However, our results show that the contribution to fast or stable dynamics is
358 not necessarily linked to species abundance as shown by the consistency in trends observed
359 across the different metrics examined that include incidence- and abundance-based indices. We
360 also examined the relationship between species traits and species abundance, but the relationship
361 was not significant (Figs. A1.7-A1.8), which also suggests that species abundance is not driving
362 the patterns observed. Thus, classification of species as core or transient is complicated and does
363 not necessarily correspond to the variation in species abundance (Coyle *et al.* 2013).

364

365 *Potential contributing factors to NE USA temperate forest dynamics*

366 Although we detected significant differences in the contribution to taxonomic turnover across
367 groups of species with differing seed mass and wood density, the results also show important

368 variation in the contribution of the species within each of the groups. Such a variation is
369 expected as the data set is highly heterogenous and represents a large area. Indeed, the observed
370 dynamics are likely the product of multiple contributing factors including diseases, natural and
371 anthropogenic disturbance, and climate change (Abrams & Nowacki, 1992; Bürgi *et al.*, 2000;
372 Coble *et al.*, 2017; Nowacki & Abrams, 1992; Wang, Larsen, & Kronenfeld, 2009). For instance,
373 the average summer temperatures in the northeastern USA has been increasing by 0.1°C per
374 decade and, in the long-term, these changes may result in shifts in forest composition and
375 dynamics (Rustad *et al.* 2012). We therefore examined the effect of precipitation and temperature
376 on temporal turnover over the 14-yr period, yet our results showed non- or weakly significant
377 trends (see Appendix S4), suggesting that trends detected in our study are unlikely to be
378 explained by climatic changes. Temperature changes so far may not be strong enough to impact
379 shifts in tree species composition for the 14-yr period studied here. Considering that trees are
380 long-lived organisms, longer-term data is necessary to thoroughly evaluate the effects of climate
381 change on forest community dynamics.

382 383 *Conclusion*

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

395
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402

403 **Authors' contribution:** MNU and NN conceived the conceptual framework. MNU and NN
404 designed the analyses, MNU conducted the analyses, JZ prepared the FIA data for analysis.
405 MNU wrote the first draft and all authors contribute significantly to the final version of the MS.

406

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

409

410 **List of appendices**

411 Appendix S1. Supplementary results.

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

413 Appendix S3. Analyses including temperature and precipitation.

414 Appendix S4. Null models.

415

416

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561

562 FIGURE LEGENDS:

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

572

573 **Fig. 2.** Boxplot showing differences in the distance, E , between trajectories that included all
574 species (ALL) and those that excluded species based on differences in seed mass (ALL w/o_{LSM} =
575 Excl. large; ALL w/o_{MSM} = Excl. medium; ALL w/o_{SSM} = Excl. small). Positive E values indicate
576 that excluded species contribute to community stability over time. Negative E values indicate
577 that excluded species contribute to community dynamism. Letters indicate the significant
578 differences among groups. The white horizontal line in the boxes indicate the median and the
579 boxes lower and upper limits represent the 25 and 75 quantiles respectively.

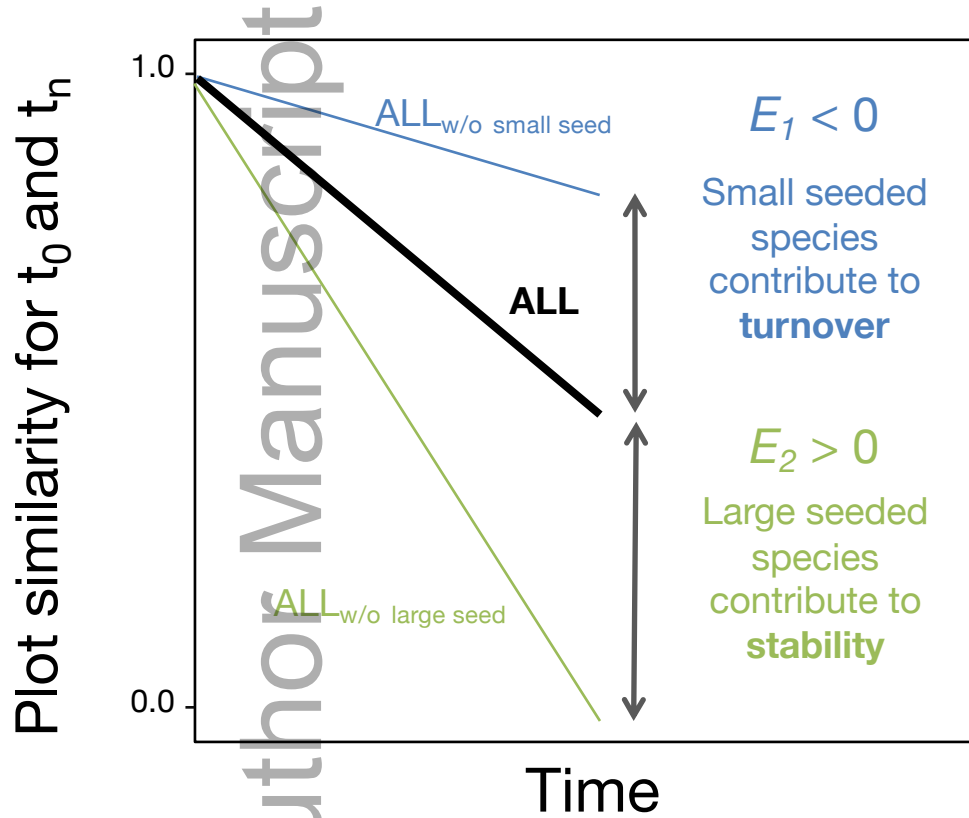
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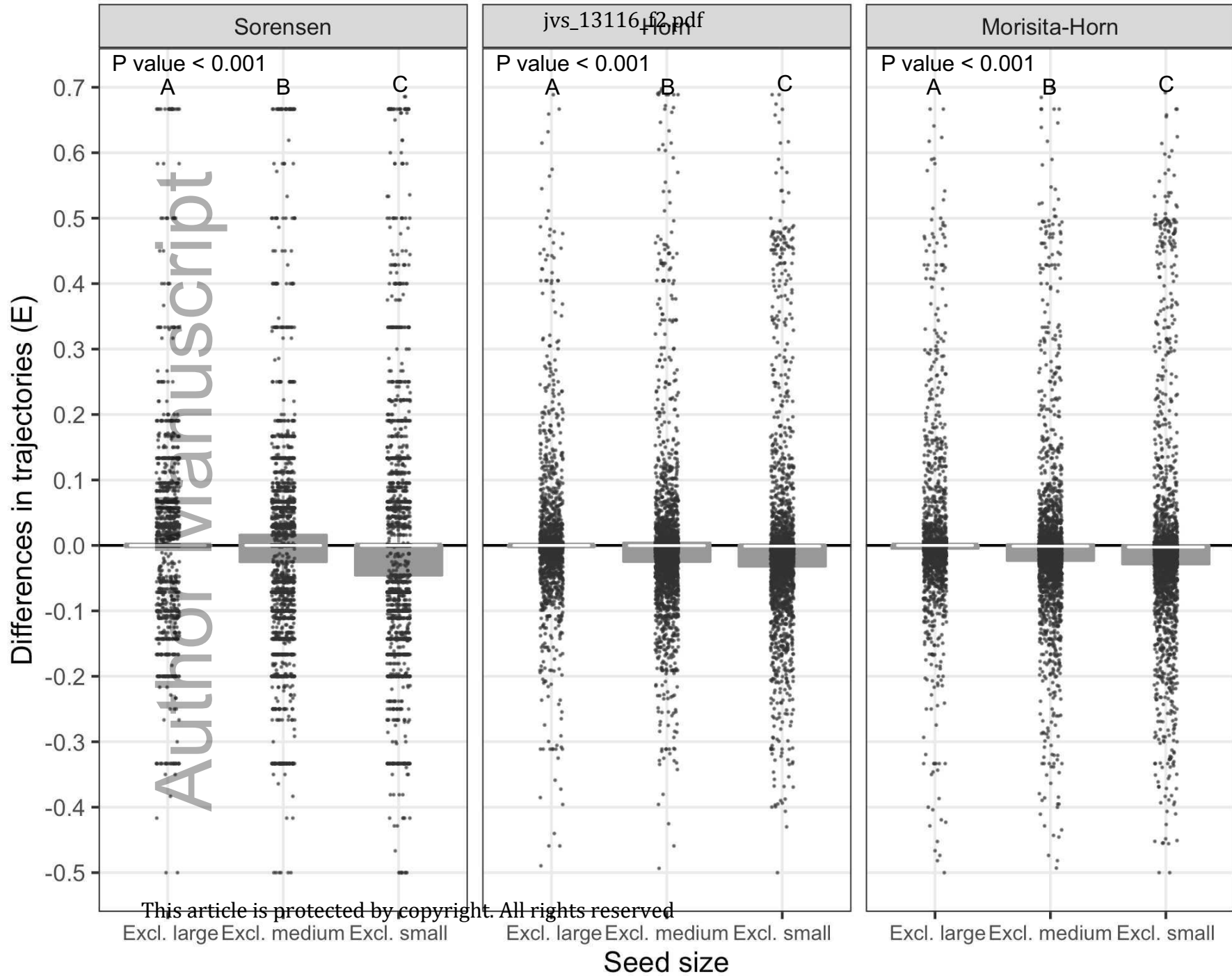
581 **Fig. 3.** Boxplot showing differences in the distance, E , between trajectories that included all
582 species (ALL) and those that excluded species based on differences in wood density (ALL w/o_{HWD} , ALL w/o_{MWD} , ALL w/o_{LWD}). Positive E values indicate that excluded species contribute to
583 community stability over time. Negative E values indicate that excluded species contribute to
584

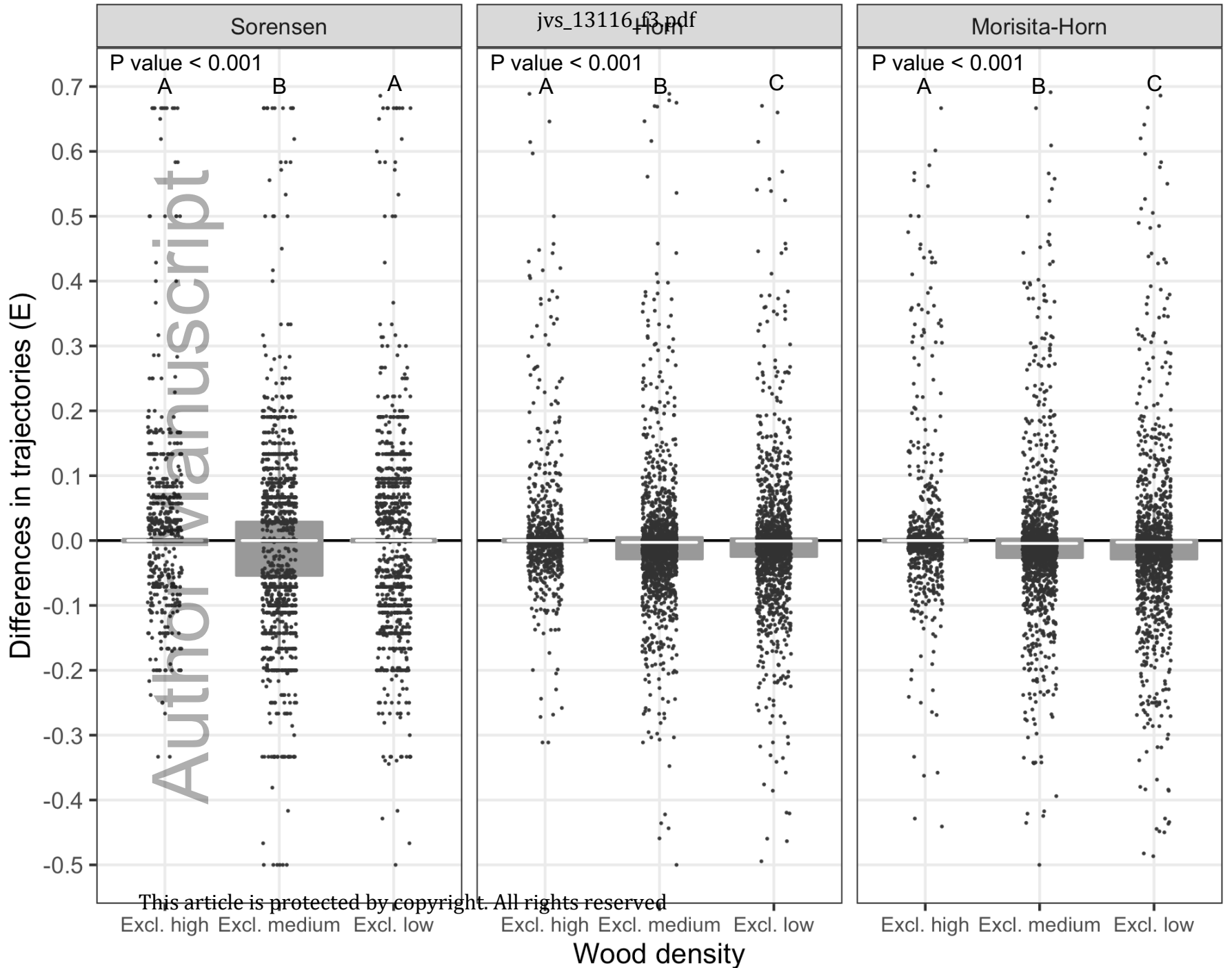
585 community dynamism. Notice that the big boxplot in the medium wood density category for the
586 Sørensen index is due to a higher number of plots that >0 turnover for this category compared in
587 the other two categories. Letters indicate the significant differences among groups. The white
588 horizontal line in the boxes indicate the median and the boxes lower and upper limits represent
589 the 25 and 75 quantiles respectively.

590

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







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Wood density

