Non-Native Plants Disrupt Dual Promotion of Native Alpha and Beta Diversity

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Abstract Non-native species can alter patterns of species diversity at multiple spatial scales, but the processes that underlie multi-scale effects remain unclear. Here we show that non-native species reduce native diversity at multiple scales through simultaneous disruption of two processes of native community assembly: species immigration, which enhances alpha diversity, and community divergence, which enhances beta diversity. Community divergence refers to the process in which local communities diverge over time in species composition because the history of species immigration and, consequently, the way species affect one another within communities are variable among communities. Continuous experimental removal of species over four years of floodplain succession revealed that, when non-native species were excluded, stochastic variation in the timing of a dominant native species' arrival allowed local communities to diverge, thereby enhancing beta diversity, without compromising promotion of alpha diversity by species immigration. In contrast, when non-native species were allowed to enter experimental plots, they not only reduced native alpha diversity by limiting immigration, but also diminished the dominant native species' role in enhancing native beta diversity. Our results highlight the importance of community assembly and succession for understanding multi-scale effects of non-native species.

Keywords Assembly rules · Leaf functional traits · Nitrogen fixers · Primary succession · Priority effect · Trait-based species sorting

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Introduction

Non-native species are increasingly recognized as a primary cause of the decline of species diversity (Mack et al. 2000; Gaertner et al. 2009; Vilà et al. 2011; Pyšek et al. 2012). Although the presence of non-native species is often correlated with native diversity, the magnitude and direction of this relationship depend on the spatial scale of observation (e.g., Stohlgren et al. 1999, 2002; Fridley et al. 2007; Sandel and Corbin 2010). In other words, native alpha (within-habitat diversity), beta (between-habitat diversity) and gamma (overall diversity integrating alpha and beta) diversities show different relationships with non-native species (e.g., Cleland et al. 2004; Davies et al. 2005). Despite considerable efforts to explain multi-scale effects of non-native species, the paucity of experimental evidence in the plant community assembly literature (Götzenberger et al. 2012) has left it unclear what processes are responsible for these effects and to what extent these apparent effects are actually caused by non-native species *per se*.

One likely but largely untested explanation for multi-scale effects is that non-native species simultaneously interfere with multiple processes that each promote native diversity, but at different scales. Consider, for example, species immigration as a process that promotes alpha diversity and community divergence as a process that promotes beta diversity. Here we define community divergence as the process in which local communities diverge in species composition for two reasons: (1) communities differ from one another in the history of species immigration and (2) the way species affect one another in a local community depends on immigration history. As local communities assemble, alpha diversity initially increases via species immigration and may remain high if immigration is frequent enough to counter extinction (MacArthur and Wilson 1967). However, given a fixed regional pool of species from which species immigrate, alpha diversity may be inversely related to beta diversity such that high alpha is automatically linked to low beta (Zobel 1997). This relationship arises because the more species local communities contain, the more similar the communities must be in species composition, particularly if local communities are randomly assembled from the regional pool (Koleff et al. 2003; Jost 2007; Vellend et al. 2007). Not all local communities are randomly assembled, however (Götzenberger et al. 2012; Rajaniemi et al. 2012). Some species may modify local habitat conditions upon arrival, and consequently influence the kind of species that can subsequently establish, facilitating some species with certain ecological traits, while inhibiting others with other traits (Weiher and Keddy 1995; Grime 1998; Lepš et al. 2001; Fukami et al. 2005). If so, local communities that vary stochastically in the timing of the arrival of key species can diverge in species composition, resulting in higher beta diversity than expected solely from environmental filtering and otherwise random assembly (Chase 2010). Thus, species immigration and community divergence, when operating concurrently, can dually promote alpha and beta diversity. If this dual promotion is realized in native communities, but disrupted when non-native species invade, this disruption may explain multi-scale effects of non-native species on native diversity. To our knowledge, this possibility has not been tested empirically.

A powerful approach to testing for this possibility would involve continuous removal of multiple species, both native and non-native, to experimentally prevent

local establishment of the removed species while otherwise allowing natural community assembly. The effects of the removed species on both alpha and beta diversity can then be evaluated. Few studies have used this type of species removal, however, despite its potential to contribute not just to the basic understanding of non-native species effects, but generally to inform ecosystem restoration efforts (Zavaleta et al. 2001). A handful of recent studies used continuous species removal and yielded new insight into invasion ecology (Hulme and Bremner 2006; Truscott et al. 2008; also see Martin and Wilsey 2012 for a related experiment involving native species addition instead of exotic species removal), but the target of continuous removal in these studies was limited to a single species.

In this paper, we present evidence that non-native species can disrupt both species immigration and community divergence, causing simultaneous reduction in native alpha and beta diversity. The evidence comes from a field study in which we established experimental plots immediately after a major disturbance and then subsequently removed particular sets of plant species (both native and non-native) continuously for 4 years in a highly invaded system in New Zealand (Bellingham et al. 2005; Peltzer et al. 2009). To test for effects of community assembly processes driven by native species and altered by non-native species, we compare native alpha, beta and gamma diversity among plots from which we removed different sets of species in a factorial fashion.

Methods

Study Site

We conducted the experiment on a river floodplain in the Kowhai River Valley, eastern South Island, New Zealand (42º20′ S, 173º33′ E, 220–280 m a.s.l.). The floodplain was sparsely vegetated as a result of flooding. Newly deposited surfaces are very low in nitrogen (N) (Bellingham et al. 2005). A native N-fixing shrub (*Coriaria arborea*, hereafter *Coriaria*) and a non-native shrub that does not fix N (*Buddleja davidii*, hereafter *Buddleja*) comprised most of the aboveground biomass during the first 10 years of primary succession (Bellingham et al. 2005). The remaining biomass consisted mainly of non-native grasses and herbs, with native woody and herbaceous plants representing only a minor component of the biomass. We previously found that non-native species were characterized by high specific leaf area (SLA), a trait usually correlated positively with relative growth rates and litter decomposition rates (Cornelissen and Thompson 1997; Shipley et al. 2006), relative to native species in this system (Peltzer et al. 2009).

Experimental Design

In January 2002, a major flood completely denuded the floodplain, providing bare surfaces for primary succession to take place (Walker et al. 2006). In April 2002, we randomly located six 50-m transects more than 1 m above water level along a 2-km stretch of the valley (Peltzer et al. 2009). Along each transect, we established eight 1 × 2 m plots spaced 4 m apart, and assigned each plot randomly to one of the following removal treatments: -C-B-E, +C-B-E, -C-B+E, -C+B-E, -C+B+E, +C-B+E, +C+B-E, and +C+B+E, where

C = *Coriaria*, B = *Buddleja*, E = all non-native species except *Buddleja*, "+" = retained, and "-" = continuously removed. All native species were retained in all plots (except *Coriaria* in appropriate plots). As some plots in one transect were lost to disturbance during the experiment, we analyzed data from the other five transects. Our removal treatment involved removing all newly germinated seedlings of the target species from the plots and from a 0.75-m buffer around the perimeter of the plots bimonthly, or ca. every 6 weeks during the growing season, from April 2002 to February 2006. Physical disturbance imposed by the bimonthly removal was minimal: removed biomass never exceeded 0.2 g total dry weight per plot.

Data Collection

Annually, we recorded the presence and cover (using the following cover classes: <1 %, 1–5 %, 6–25 %, 26–50 %, 51–75 %, 76–95 % and >95 %) of all plant species rooted within each plot in December. We then destructively harvested plots in February 2006. To this end, we first trimmed and removed all plant material outside a 0.7 × 1.7 m area centered inside each plot to minimize edge effects. We then collected aboveground biomass for all plant species contained within the 0.7 × 1.7 m area, and determined the dry mass of each species (Peltzer et al. 2009). We also collected fresh foliage of 40 plant species (14 native species and 26 non-native species) to measure foliar N and P concentrations in order to facilitate trait-based interpretation of community divergence (Weiher and Keddy 1995; Shipley et al. 2006; Ackerly and Cornwell 2007). Together, the 40 species comprised >99 % of the total aboveground biomass, and the 14 native species also comprised >99 % of the total native aboveground biomass in the system. We measured total foliar N and P concentrations (%) using automated colorimetric methods (Technicon Instruments 1977). Leaves of each species were sampled from at least 10 individual plants found at the same stage of succession as the experimental plots but located outside the plots.

Diversity Calculation

Using destructive harvest data from February 2006 on the native species for which leaf trait data were available, we calculated alpha, beta and gamma diversity of native plants. Alpha diversity was measured as the number of native species observed per plot. Simpson's diversity index yielded qualitatively the same results as species richness. Our measure of beta diversity was the dissimilarity of native species composition between plots within treatments, quantified as the mean distance to individual plots from the group centroid, calculated according to the distance matrix based on Jaccard dissimilarity (Anderson 2004, 2006; Anderson et al. 2006). Bray-Curtis dissimilarity, which takes into account species biomass, yielded qualitatively the same results as Jaccard dissimilarity, which considers only the presence and absence of species. Numerous measures of beta diversity have been proposed, each with different strengths and limitations (Koleff et al. 2003; Jost 2007, 2010; Tuomisto 2010; Veech and Crist 2010; Wilsey 2010). We used Anderson's (2006) measure because it allows between-treatment difference in beta diversity to be statistically tested and is robust and powerful under a variety of conditions (Anderson 2004, 2006; Anderson et al. 2006; Chase 2007, 2010). Gamma diversity was measured as the total number of native species observed in

treatments. Although *Coriaria* is a native species, because it was part of the removal treatments, we excluded it from calculations of native diversity.

Statistical Analysis

In treatment +C-B-E, all native species were allowed to establish, while all non-native species were excluded. We compared this wholly native treatment with other treatments to test for the effects of establishment of *Coriaria*, *Buddleja* and other non-native species on native diversity. We examined removal treatment effects using ANOVA followed by Tukey's HSD test for alpha diversity, using PERMDISP followed by pair-wise *a posteriori* test (Anderson 2004; Anderson et al. 2006) for beta diversity, and using *t*-tests (to compare plots where all non-native species were excluded and those where all or some non-native species were retained) for gamma diversity. To ensure our results were not biased by exclusion of rare species, we repeated these analyses using all species recorded in plots instead of including only species for which leaf trait data were available.

It has been pointed out that beta diversity is often not independent of alpha diversity (Koleff et al. 2003; Jost 2007; Vellend et al. 2007). For example, if species are randomly distributed in plots from a common pool of potential colonizers, the smaller the number of species that are distributed per plot (i.e., lower alpha diversity), the more variable the set of species will be between plots (i.e., higher beta diversity). For this reason, in order to compare beta diversity between experimental treatments differing in mean alpha diversity, it is informative to generate a null expectation of beta diversity under different levels of mean alpha diversity, so that observed beta diversity can be examined in light of the null expectation that is corrected for alpha diversity. To this end, we conducted a null model analysis similar to the approach developed by Raup and Crick (1979). Specifically, we first used the data reported in Bellingham et al. (2005: Appendix 2) to estimate the regional frequency of the occurrence of each native species recorded in our experimental plots. The regional frequency of each species was calculated by averaging the observed occurrences of the species across all four developmental stages of the floodplain vegetation (open, young, vigorous and mature stages) identified by Bellingham et al. (2005), taking into account the relative abundance of the developmental stages at the study site. We then generated, for each of the eight experimental treatments, 1,000 sets of null communities by randomly assigning species to plots, with the probabilities of drawing species determined by their regional frequencies estimated as above, while keeping alpha diversity within the experimental treatment the same as observed. Null communities were generated using Mathematica 7.0 (Wolfram Research, Champaign, Illinois, USA). We then used PERMDISP (Anderson 2004) to calculate beta diversity for each set of null communities.

Results

Native Alpha Diversity

When non-native species were prevented from establishing (Fig. 1a), native alpha diversity increased over time as more species arrived. When non-native species were
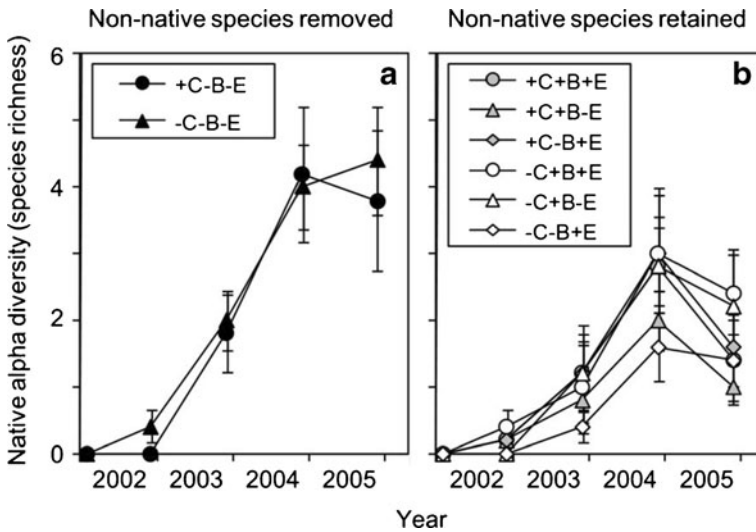
Fig. 1 Temporal changes in native alpha diversity, measured as within-plot (2 m²) native plant species richness (means with 1 SEM, $n=5$ for each treatment), in the absence (**a**) and presence (**b**) of non-native species after a flood denuded the floodplain in January 2002. Graphs show data collected in December 2002–2005. Native alpha diversity increased more from 2002 to 2003 ($t=3.82$, $P_{\text{one-tailed}}<0.01$) and from 2003 to 2004 ($t=2.47$, $P_{\text{one-tailed}}<0.02$) and declined less from 2004 to 2005 ($t=2.13$, $P_{\text{one-tailed}}<0.04$) in the absence of non-native species (**a**) than in their presence (**b**). Codes refer to bimonthly species-removal treatments: C – the native shrub, *Coriaria arborea*, B – the non-native shrub, *Buddleja davidii*, E – non-native plants other than *Buddleja*, + – retained, - – continuously removed. Native species richness shown does not include *Coriaria*

allowed to establish (Fig. 1b), native alpha diversity increased to only about half as much as when non-native species were prevented from establishing. After 4 years of community assembly (Fig. 2a), native alpha diversity was highest when only native species except *Coriaria* were allowed to establish (treatment -C-B-E). Retaining *Coriaria* (treatment +C-B-E) did not significantly reduce native alpha diversity from the level of this highest treatment (black bars in Fig. 2a), whereas retaining non-native species often resulted in a significant reduction of native alpha diversity from the level of the highest treatment, particularly in treatment -C-B+E. These results are for the species for which we have leaf trait data, but hold qualitatively when all species recorded are included in the analysis.

Native Beta Diversity

In contrast to results for native alpha diversity, native beta diversity was lowest when only native species except *Coriaria* were allowed to establish (treatment -C-B-E; Fig. 2b). Retaining *Coriaria* (treatment +C-B-E) resulted in a significant increase in native beta diversity (Fig. 2b). Retaining non-native species (grey and white bars in Fig. 2b) also increased native beta diversity compared with treatment -C-B-E, but not any more significantly than retaining *Coriaria* did (treatment +C-B-E; Fig. 2b). As with native alpha diversity, these results for native beta diversity hold qualitatively when all species recorded in plots are included in the analysis.
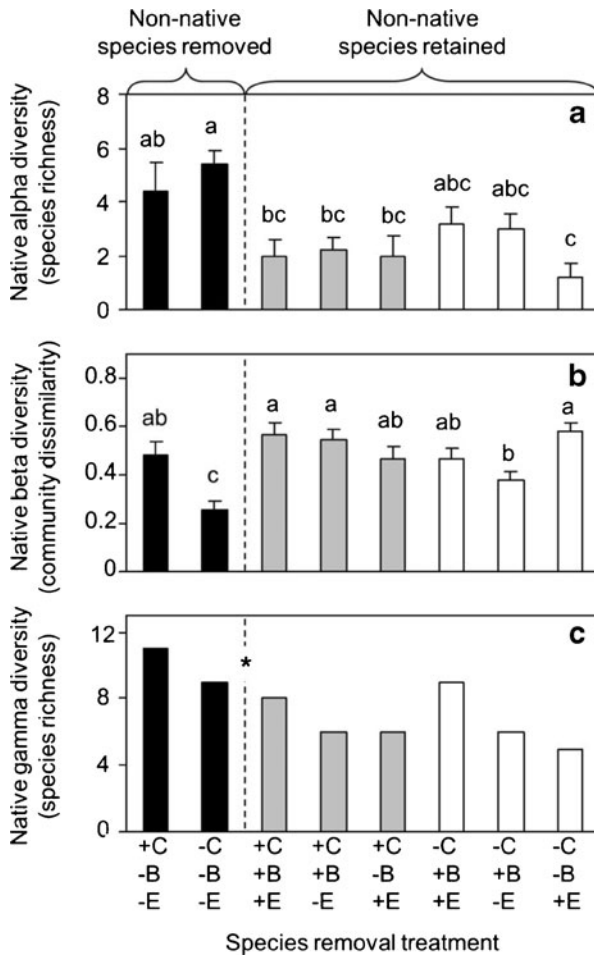
Fig. 2 Alpha, beta and gamma diversity of native plants at the end of the 4-year exclusion experiment (February 2006). Alpha diversity (**a**) is expressed as within-plot native species richness. Beta diversity (**b**) is expressed as between-plot community dissimilarity (Jaccard dissimilarity) of native species within treatments. Gamma diversity is expressed as the number of all species recorded in at least one plot (**c**). *Coriaria* is not included in calculation of alpha, beta or gamma diversity. The same letters denote no significant difference between treatments ($P>0.05$), determined by Tukey's HSD test after ANOVA for alpha diversity (**a**) and by pair-wise *a posteriori* test after PERMDISP (Anderson 2004) for beta diversity (**b**). For gamma diversity (**c**), asterisk denotes significant difference between treatments where all non-native species were removed and treatments where all or some non-native species were retained ($t=2.74$, $P<0.03$). Values are shown as means + 1 SEM. Treatment codes are as in Fig. 1

Native Alpha vs Beta Diversity

Despite these significant differences observed between treatments (Fig. 2), native beta diversity was consistently indistinguishable from the null expectation corrected for native alpha diversity in all but one treatment (Fig. 3). Only in the wholly native treatment (treatment +C-B-E) did native beta diversity deviate significantly from the null expectation, with the observed value (black circle in Fig. 3) significantly higher than expected.
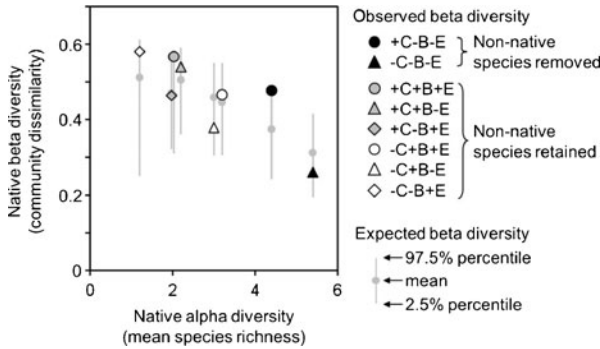
Fig. 3 Expected and observed relationships between native beta diversity (between-plot community dissimilarity) and native alpha diversity (mean within-plot species richness). Data points represent treatment groups observed at the end of the 4 yr exclusion experiment (February 2006). Treatment symbols are as in Fig. 1. For each observed mean alpha diversity, we indicate both the value of observed beta diversity and the mean value of expected beta diversity calculated from null model analysis, with the range between the 2.5 and 97.5 % percentiles of the randomized distribution of expected beta diversity (see Methods). Null model analysis revealed that +C-B-E (black circle) was the only treatment in which observed beta diversity was significantly higher ($P<0.05$) than the null expectation.

Native Gamma Diversity

Native gamma diversity was higher when non-native species were removed than when all or some non-native species were retained (Fig. 2c).

Non-Native diversity

When non-native species were retained in plots, species removal treatments had no significant effect on alpha, beta or gamma diversity of non-native species (Fig. 4).
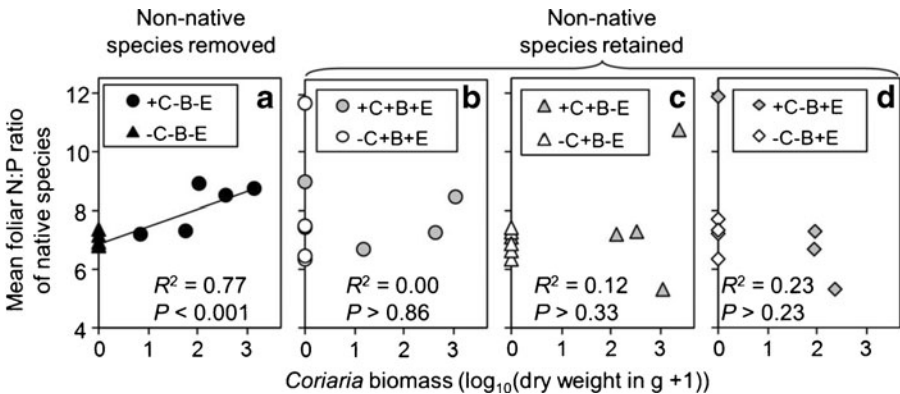

Fig. 4 Alpha, beta and gamma diversity of non-native plants at the end of the 4 yr exclusion experiment (February 2006). Diversity was measured and tested for significant difference as in Fig. 2. *Buddleja* is not included in calculation of alpha, beta or gamma diversity. No significant effect of species removal treatment was detected (denoted by n.s.)

Coriaria *Biomass and Foliar N:P*

Coriaria biomass and mean foliar N:P of native plants were significantly correlated when non-native plants were removed (Fig. 5a), whereas no significant relationship was detected when non-native species were retained (Fig. 5b,c,d).

Discussion

Our results provide experimental evidence that non-native species suppressed two diversity-enhancing processes of native community assembly, species immigration and community divergence. To explain this key finding of our study, below we will use our results to argue that, in native community assembly, spatial variation in *Coriaria*'s time of
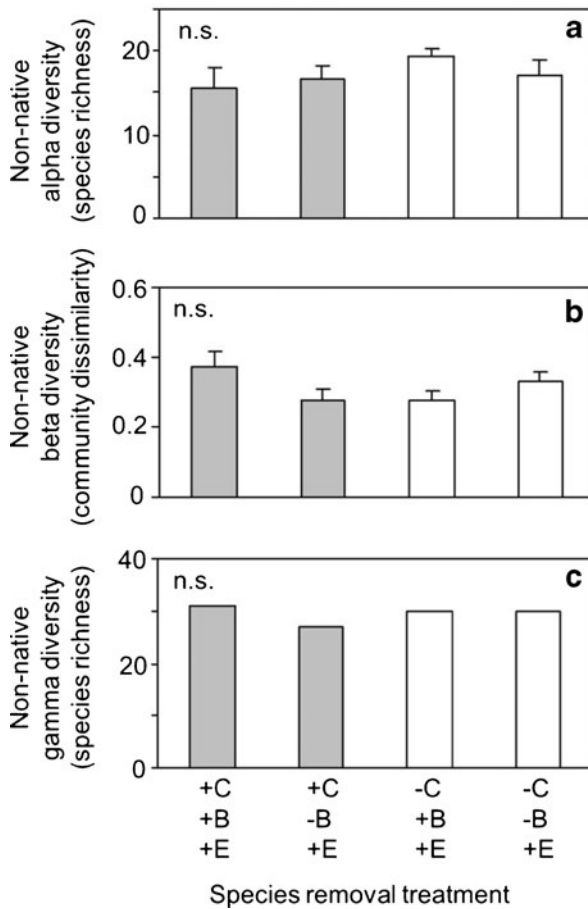

Fig. 5 Relationships between *Coriaria* biomass and mean foliar N:P of native species in plots where only native species were retained (**a**), where non-native species were also retained (**b**), where *Buddleja* (but no other non-native species) was also retained (**c**), and where non-native species other than *Buddleja* were also retained (**d**). Data points represent plots observed in February 2006. Regression line is shown where significant. Treatment symbols are as in Fig. 1

arrival may have led to variation in the degree of habitat modification by this species, causing different species to establish in different plots according to their ecological traits (Stubbs and Wilson 2004; Holdaway and Sparrow 2006; Wilson and Stubbs 2012) and ultimately increasing beta diversity more than expected from random assembly (Fukami et al. 2005; Lanta and Lepš 2009; Chase 2010). This biotic increase in beta diversity occurred without compromising enhancement of alpha diversity by immigration. We will further argue that non-native species not only reduced native alpha diversity by competitive exclusion, but also diminished *Coriaria*'s role in enhancing native beta diversity.

Native Alpha Diversity

The high native alpha diversity in the native-species-only treatments (+C-B-E and -C-B-E), in contrast to the low native alpha diversity in the presence of non-native species (Fig. 2a), suggests competitive exclusion of native species by non-native species (Seabloom et al. 2003). Possible mechanisms of competitive exclusion include reduced sites available for germination (Walker et al. 2003) and limiting access to water, nutrients or both (Stubbs and Wilson 2004; Bartelheimer et al. 2010; Everard et al. 2010). The lack of significant reduction of native alpha diversity by *Coriaria* (Fig. 2a) may seem surprising, given that *Coriaria* biomass was greater than that of all other species combined. Our previous work suggests, however, that *Coriaria* is unlikely to negatively affect native alpha diversity even after 30 years of primary succession (Bellingham et al. 2005). If competitive exclusion by *Coriaria* were to happen over a longer term than our experiment (i.e., >4 yr), our results (Fig. 1) suggest that competitive exclusion by non-native species takes place more rapidly (i.e., within 4 years), thereby shortening the time window of enhanced native alpha diversity. Regardless, 4 years of primary succession is a relevant time scale to evaluate community assembly in this system because floods routinely destroy most plant communities on this floodplain every 5–15 years (Bellingham et al. 2005).

Native Beta Diversity

Between the two native-species-only treatments, the higher beta diversity observed in +C-B-E than in -C-B-E (Fig. 2b) may be explained in terms of *Coriaria*'s potential to modify local nutrient conditions (Walker et al. 2003). As the dominant N-fixer, *Coriaria* can alleviate the strong N limitation that exists in newly deposited surfaces after a flood (Bellingham et al. 2005). Given variation among plots in the time of *Coriaria*'s arrival (see variation across *x*-axis in Fig. 6), *Coriaria*-induced variation among plots in the level of N limitation may have provided opportunities for different sets of species with varying degrees of N demand to establish in different plots. For example, as *Coriaria* biomass increases, species with higher N:P requirements may become more likely to establish (Güsewell 2004). If *Coriaria* was continuously prevented from establishing, communities would be predicted to consist of species with lower leaf N:Ps. These communities should also have smaller between-plot variation in foliar N:P than the communities in which *Coriaria* was allowed to establish. Although the exact mechanisms that control beta diversity remain unknown, we found patterns that are strongly consistent with each of the above predictions regarding *Coriaria*-driven species sorting according to foliar N:P
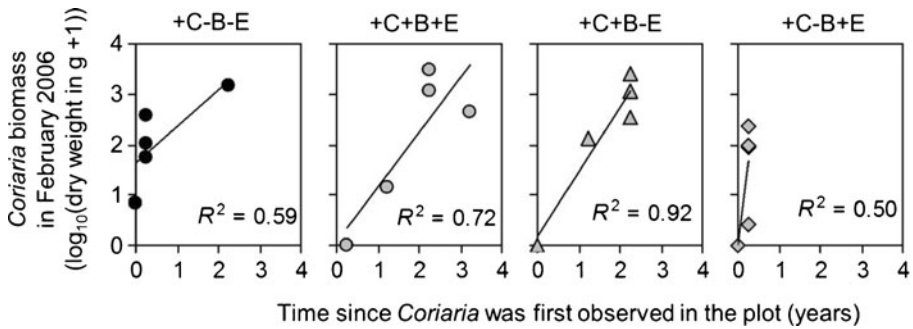
Fig. 6 Relationships between time since *Coriaria* was first observed and the biomass of *Coriaria* at the February 2006 harvest. Each data point represents a plot. Treatment symbols are as in Fig. 1

(Fig. 5a). Moreover, we also found that the time since the first arrival of *Coriaria* explained most (68 % on average) of the between-plot variation in *Coriaria* biomass within treatments (Fig. 6), suggesting that the main source of variation in *Coriaria* biomass was indeed the time of their arrival (Bellingham et al. 2005; Walker et al. 2006). If so, the *Coriaria*-driven assembly of native communities is historically contingent in species taxonomic composition but deterministic in species trait composition (Fukami et al. 2005), a phenomenon that contributes to increased beta diversity (Chase 2010).

Non-native species appear to have disrupted the enhancement of native beta diversity that results from variation in *Coriaria* immigration, as suggested by the lack of significant relationships between *Coriaria* biomass and mean foliar N:P of native plants when non-native species were retained (Fig. 5b,c,d). We speculate that, in the native-species-only treatments (Fig. 5a), alleviation of N limitation by *Coriaria* operated at a highly local scale within plots (i.e., within the rooting zone). We base this speculation on our previous finding that, at the 1 × 2 m plot scale, no significant effect of *Coriaria* on soil N availability was apparent during 4 years of primary succession in this system (Peltzer et al. 2009). We also know that at a 3 × 3 m plot scale, it takes 10 years or longer for *Coriaria*'s effect on soil N to emerge (Bellingham et al. 2005). It appears then that *Coriaria*'s role in enhancing native beta diversity (Figs. 2b, 3) was so local and subtle that it was overruled by competitive exclusion of native species by non-native species. In contrast, neither the diversity (compare grey and white bars in Fig. 4) nor the effect on native species diversity (compare grey and white bars in Fig. 2) of non-native species was greatly affected by *Coriaria*. The asymmetrically strong effect of non-native species is surprising because their collective biomass is much less than that of *Coriaria* (Peltzer et al. 2009), and suggests that subordinate species (*sensu* Grime 1998) can more strongly control community assembly and diversity than generally thought, likely through rapid tissue turnover and decomposition as inferred from relatively high SLA and foliar N concentrations for non-native species (Peltzer et al. 2009).

Notably, *Coriaria* was not the only N-fixer in the system, but some non-native species were also N-fixers (e.g., *Trifolium* and *Vicia* spp.). Despite their low biomass, non-native N-fixers can add more N to the soil than *Coriaria*, more likely because of their relatively rapid tissue turnover and decomposition rates, at least at the 1 × 2-m plot scale (Peltzer et al. 2009). Our results for native diversity suggest then that the

dual negative effects that non-native species exerted on native alpha and beta diversity overwhelmed any of the potentially positive effects that non-native species may have had on native beta diversity through N addition.

Native Alpha vs *Beta Diversity*

If non-native species disrupt *Coriaria*'s role in enhancing native beta diversity (Fig. 5b,c,d), why was native beta diversity high between the plots where non-native species were allowed to establish (grey and white bars in Fig. 2b)? It seems that high native beta diversity in the presence of non-native species is simply a result of statistical inevitability, where low alpha diversity automatically results in high beta diversity (Koleff et al. 2003; Jost 2007; Vellend et al. 2007), as supported by our null model analysis (Fig. 3). The wholly native treatment (treatment +C-B-E) was the only exception to the general negative relationship between native alpha and beta diversity: retaining *Coriaria* appears to have released the native community from the statistical trade-off between alpha and beta diversity, as shown by the significant deviation of beta diversity from expected values (black circle in Fig. 3), coupled with increased gamma diversity (Fig. 2c). Taken together, these results suggest that *Coriaria* drives community divergence, thus increasing beta diversity more than expected from random assembly (Fig. 3) despite a high level of alpha diversity maintained by species immigration (Fig. 2a). Importantly, this significant community divergence was realized only when all non-native species were experimentally excluded from plots.

Previously, we showed that co-occuring non-native species in this system had functional traits related to resource acquisition (i.e., high foliar N, high SLA) that differ from co-occruring native species (Peltzer et al. 2009; Kurokawa et al. 2010). Therefore, although we have focused on patterns of diversity in this study, the multi-scale effects of non-native species we have described here may have broader implications for ecosystem functioning, affecting productivity, decomposition, and nutrient cycling (Van der Putten et al. 2000; Lepš et al. 2001).

Conclusion

This study is the first, to our knowledge, to demonstrate that non-native species disrupt multi-scale diversity enhancement by species immigration and community divergence. What made this demonstration possible was the experimental approach involving continuous removal of multiple species. Our findings support the view that the consequences of non-native species invasions for native species diversity can be best understood within the context of biotically driven succession (Rejmánek and Lepš 1996; Meiners et al. 2009; Simberloff 2010; Tognetti et al. 2010). Although this view may seem obviously correct given that most communities are likely in a transient state, rather than in an equilibrium state (Fukami and Nakajima 2011, 2013), relatively little effort has been made to experimentally evaluate non-native species impacts from a succession perspective (Davis et al. 2005). We suggest that applying experimental approaches similar to the one we have used here to a variety of other systems will help to further clarify the importance of community assembly processes for explaining multi-scale effects of non-native species on native diversity.

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