

RESEARCH ARTICLE

Functional Ecology



Exotics are more complementary over time in tree biodiversity–ecosystem functioning experiments

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Abstract

1. The Biodiversity–Ecosystem Functioning (BEF) literature proposes that ecosystem functioning increases with biodiversity because of complementarity in resource-use among species, associated with functional diversity. In this study, we challenge the trait-based ecology framework by comparing congeneric exotic (European) and native (North American) tree species showing similar resource-use functional trait values. The trait-based framework suggests that two functionally equivalent species should play similar roles in a community, resulting in similar interactions and performances. However, several studies showed that when growing in mixtures, exotic species that are functionally equivalent to native species benefitted from enemy release, resulting in a reduced apparent competition. We hypothesize that exotic species should be more productive than native species because the exotic species benefit from reduced apparent competition due to enemy release rather than from possessing more competitive resource-use functional traits.
2. We study a diversity experiments, part of the International Diversity Experiment Network with Trees (IDENT), composed of two identical sites, each with two orthogonal diversity gradients: species richness and functional diversity. The functional gradient consists of species combinations of equal richness but increasing functional diversity, using different combinations of species provenance to assess the relationship between productivity, functional diversity and species provenance, independently of species richness. We grew a total of 12 species (six native and six exotic) in different combinations of one-, two- and six-species mixtures. The exotic species were selected based on their functional equivalence to their native congeneric species.
3. Eight years after planting, we found that exotic species were more productive than native species, but only at high functional diversity. Results indicate that exotic species overall benefit from a reduced apparent competition, and that exotic-increased productivity at high functional diversity is consistent with the enemy release hypothesis.
4. After 8 years, exotic species were more productive overall than their native counterparts, but only in the most functionally diverse communities. This study

represents a first step in understanding the relative importance of complementarity in resource-use and apparent competition in a context of an exotic tree species invasion.

KEYWORDS

apparent competition, biodiversity experiment, enemy release hypothesis, exotic, functional diversity, IDENT, native, productivity

1 | INTRODUCTION

The Biodiversity–Ecosystem Functioning (BEF) literature proposes that ecosystem functioning increases with biodiversity because of complementarity in resource-use among species (Grossman et al., 2018). This positive relationship has been studied for more than two decades with contrasting results, both supporting (e.g. Balvanera et al., 2006; Cardinale et al., 2007; Hooper et al., 2005; Liang et al., 2016) and refuting (e.g. Sandau et al., 2019; Thompson et al., 2005). It has been proposed that functional diversity and community-weighted means of trait values (hereafter functional identity) may be better predictors of ecosystem functioning than species richness because they more closely relate to selection and complementarity mechanisms. The challenge is, however, to tease apart the effects of species richness, functional diversity and functional identity. These three aspects of community structure tend to be correlated in most of both natural communities and biodiversity experiments; hence, specific experimental designs are required to disentangle these effects (Tobner et al., 2014).

Functional diversity and functional identity are two properties of communities summarizing competition and complementarity among species. Resource-use complementarity occurs when two species have different functional traits values allowing them to use resources differently (Loreau, 1998). Inversely, resource-use competition should be maximal if two species express similar trait values, therefore complementarity should be null. At the community level, increasing species richness by adding a species with similar trait values as another species already present in the community should have no effect on productivity (Maire et al., 2012). However, trophic complementarity may also arise from shared enemies or mutualists, or from diversity effects that increase protection from disease or herbivory (Cobb et al., 2010; Poisot et al., 2013; Van der Plas, 2019). Even if two species share similar resource-use trait values, they may be complementary to each other if they have distinct enemies such as herbivores or pathogens (Figure 1). Alternatively, two species may severely compete with each other (here we use the word ‘compete’ in terms of outcomes of interactions, not specifically about resource-use competition) even if they exploit different resources because they share enemies (with different vulnerability to those enemies) and interact by apparent competition (Gravel et al., 2016). Positive relationship between productivity and functional diversity may thus occur from either resource-use or trophic complementarity. Several studies have empirically investigated the impact of diversity at

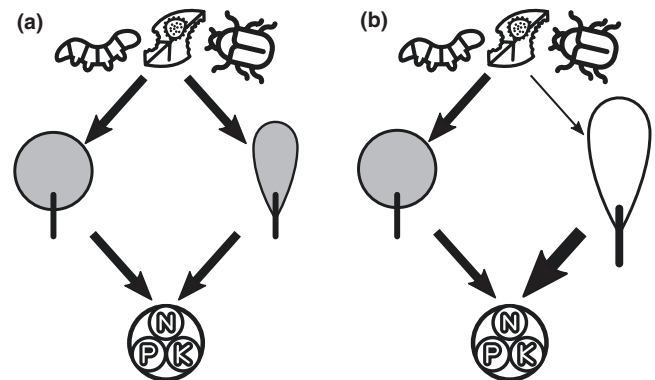


FIGURE 1 Apparent competition and complementarity in a two tree species community. (a) Both tree species are native (middle). The herbivores/enemies (top) negatively consume/impact both species equally, resulting in apparent competition. Both species also use the same resources and therefore interact by exploitative competition (bottom). (b) One species is native (grey) and the other is exotic (white). The exotic species use the same resources as its native counterpart due to similar resource-use functional traits values. The herbivores/enemies negatively consume/impact the native species more than the exotic species and therefore apparent competition on the exotic is less important than in A due to difference in defence level. The exotic species productivity and resource-use increases over time to become dominant

several trophic levels, but the contribution of trophic complementarity and apparent competition to BEF has yet to be tested.

Exotic species provide an unique opportunity to investigate the contribution of both functional and trophic complementarity to BEF. Exotic species may be used to push the trait-based approach and the complementarity hypothesis further: If only resource-use traits define complementarity, then native species and functionally equivalent exotics should be interchangeable in a community with no impact on ecosystem functioning. Alternatively, if other characteristics of exotics that are not accounted for in resource-use functional diversity indices are also impacting ecosystems functioning, then introducing exotics in a mixture (experimental or through actual invasion in natural systems) could significantly alter the strength of the relationship. A common hypothesis to explain such exotic superiority is that exotics are less consumed by predators and/or diseased by pathogens and therefore may experience some degree of enemy release because local enemies did not co-evolve with them (Meijer et al., 2016). Therefore, an exotic species could potentially be functionally equivalent to a native species at a resource-use level

but distinct from natives at a defence level (Figure 1). The problem is that the traits involved in interactions with higher trophic levels (e.g. leaf defence compounds, root chemical signals) are often difficult, if not impossible, to measure and contrary to resource-use traits are rarely incorporated in the computation of functional diversity indices. Disentangling functional and trophic complementarity and their effects on productivity requires experiment designed specifically to this purpose.

The goal of the International Diversity Experiment Network with Trees (IDENT) is to investigate the relationship between biodiversity and ecosystem functioning at multiple hierarchical levels within communities (Tobner et al., 2014). IDENT includes several sites across North America and Europe and uses a replicated design of high-density tree plots of varying functional diversity combinations for a given set of species richness levels. The IDENT Auclair-Cloquet (AuCI) experiment in particular was designed to focus on the effect of exotic species on the functional diversity–ecosystem functioning relationship. At the core of the design are two orthogonal gradients: a gradient of functional diversity and a gradient of species richness comprising two- and six-species mixtures and all monocultures, from a pool of six native tree species (from eastern North America) and six exotic (European) functional equivalents. In the presence of some form of enemy release, we expect the exotic and native species to differ in their productivity due to their interactions at different trophic levels, despite similarities in their exploitative traits values. Recent studies have confirmed that exotic plants suffer less from soil microbial feedback, attacks by fungal and viral pathogens and herbivores in their introduced ranges than in native areas (Agrawal et al., 2005; Mitchell & Power, 2003; Nguyen et al., 2016; Raymond-Léonard et al., 2018; Wein et al., 2016). Although herbivory or interaction with mycorrhiza and bacteria was not measured in this experiment, comparing the productivity of species from the same genus but from different provenance is a first step in investigating the complex balance of positive and negative effects on resources and trophic complementarity.

Our objective in this study was to investigate the relationship between functional diversity and ecosystem functioning. We used native species and their exotic equivalents to challenge the hypothesis that ecosystem functioning could be explained by functional traits only. We first predict that ecosystem functioning should increase as functional diversity increases in mixtures of two and six species, irrespective of the origin of the species. We further consider the trophic complementarity hypothesis, assuming that reduced interaction with local enemies do promote resource-use complementarity among exotic and exotic-native pairs. As a consequence, we predict that the diversity–ecosystem functioning relationship will be stronger for exotic and exotic-native mixtures than for native-only mixtures. These predictions stem from the idea that complementarity of all forms among species promotes resource-use and therefore ecosystems functioning. Furthermore, based on observations that diversity effects on biomass production increased over time (Cardinale et al., 2007; Reich et al., 2012 in grasslands), we expect that the differences between exotic and native species in the

functional diversity–ecosystem functioning relationship will also increase over the duration of the experiment.

2 | MATERIALS AND METHODS

2.1 | IDENT overview

The IDENT Auclair-Cloquet (AuCI) experiment, established in 2010, is part of the 'International Diversity Experiment Network with Trees (IDENT)' (described in Tobner et al., 2014). The AuCI experiment was specifically implemented to tackle the question of native versus exotic species effect on the functional diversity–ecosystem functioning relationship. AuCI includes three pairs of angiosperm and three pairs of gymnosperm tree species sharing the same genus and similar trait values (more below) but made up of a North American and a European species (12 species from six genera including one native and one exotic per genus; Table 1). North American and European species pairs are more or less equivalents in traits values, relative to all other species from the pool, but not exactly the same. The experimental design consists of plots with one-, two- or six-species mixtures (Table S1). Species combinations were chosen to create two orthogonal gradients of taxonomic richness and functional diversity. Communities of two and six species were chosen to maximize the functional diversity gradient and to balance representation of North American and European species. The traits used in the functional diversity calculation, described later, are related to resource-use and light capture (Díaz et al., 2016).

2.2 | Experimental site and design

The study took place at two sites established in 2010, one near Auclair (Québec, Canada; 47°41'47.8"N 68°39'22.7"W) and the other in Cloquet (Minnesota, USA; 46°42'18.3"N 92°31'29.9"W). Auclair was established on a low-input abandoned pasture with loam soil, while Cloquet is on a previously forested site (red and white pine and mixtures of aspen, spruce, balsam, birch and hazelnut) with sandy loam soil. Auclair is characterized by an annual precipitation of 965 mm and a mean temperature of $2.325 \pm 11.0^\circ\text{C}$, whereas Cloquet is characterized by an annual precipitation of 881 mm and a mean temperature of $5.02 \pm 11.4^\circ\text{C}$. The precipitation regime is relatively stable during the year at Auclair with a monthly mean of $80.4 \text{ mm} \pm 10.6 \text{ mm}$. At the Cloquet site, precipitation is low in the winter and high in the summer with a monthly mean of $73.4 \text{ mm} \pm 37.6 \text{ mm}$. Both sites are about 0.5 ha each with ~10,000 seedlings planted. Each site has a four-block repetition made of 48 plots each. Mixtures position within blocks as well as trees within plots were randomized. The 48 plots include 12 monocultures, 30 two-species mixtures and 6 six-species mixtures. Trees were planted in plots of 7 by 7 trees 40 cm apart to stimulate interactions among trees and associated organisms (mycorrhiza, insects, soil micro-organisms). We considered only the 3×3 central trees of each plot in the analysis, to avoid edge effect from neighbouring plots. Each block is surrounded by a buffer of randomly selected tree species

TABLE 1 Species provenance and species mean functional trait values

Genus	Species	Code	Provenance	SLA	SM	WD	LDMC	LNC _{area}	LNC _{mass}
<i>Acer</i>	<i>Saccharum</i>	ACSA	North America	19.949	2.106	0.623	0.386	1.061	18.689
<i>Acer</i>	<i>Platanoides</i>	ACPL	Europe	20.643	1.816	0.557	0.339	0.958	22.118
<i>Betula</i>	<i>Papyrifera</i>	BEPA	North America	16.332	-0.503	0.540	0.289	1.420	23.139
<i>Betula</i>	<i>Pendula</i>	BEPE	Europe	17.586	-0.345	0.550	0.301	1.800	25.665
<i>Larix</i>	<i>Laricina</i>	LALA	North America	8.673	0.786	0.530	0.315	1.895	16.255
<i>Larix</i>	<i>Decidua</i>	LADE	Europe	10.577	0.224	0.484	0.339	2.068	20.754
<i>Picea</i>	<i>Glauca</i>	PIGL	North America	4.509	0.810	0.381	0.377	3.005	12.084
<i>Picea</i>	<i>Abies</i>	PIAB	Europe	5.438	0.331	0.392	0.354	3.656	12.683
<i>Pinus</i>	<i>Strobus</i>	PIST	North America	7.668	1.174	0.355	0.338	2.901	14.482
<i>Pinus</i>	<i>Sylvestris</i>	PISY	Europe	4.553	0.947	0.433	0.306	2.753	13.264
<i>Quercus</i>	<i>Rubra</i>	QURU	North America	13.158	3.322	0.610	0.395	1.502	20.147
<i>Quercus</i>	<i>Robur</i>	QURO	Europe	14.496	3.398	0.622	0.373	2.643	23.840

SLA (Specific Leaf Area) mm²/mg, SM (Seed mass; log (g per 1000 seeds)), WD (Wood density; g/cm³), LDMC (Leaf Dry Matter Content; g/g), LNC_{area} (Leaf Nitrogen content per unit area; g/m²), LNC_{mass} (Leaf Nitrogen content per unit mass; mg/g).

from the experiment species pool (Figure S1). All seedlings for both sites came from public nurseries in Québec, produced from the same stock, sorted by size and quality into homogeneous units. Bags were separated at random into two lots before being transported to the sites in refrigerated trucks to each site. Seedlings were planted on both sites less than a week apart in spring 2010.

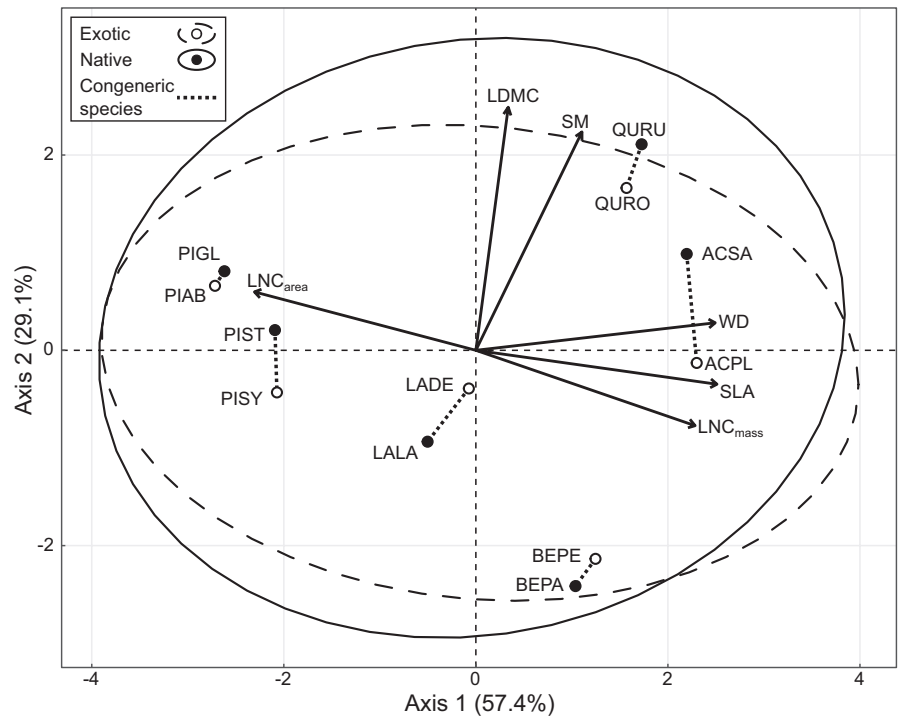
2.3 | Trait selection and diversity indices

We calculated mean species trait values for 15 traits related to leaves, stems and roots (Figure S2) using the IDENT trait database (Belluau, 2020; a complete list of references is provided in the figshare repository) to compute a new functional diversity specifically related to this experiment. At that time, we lacked functional traits measured in situ for some species and had to supplement our traits with online databases. We performed a stepwise backward selection of traits to minimize the distance between pairs of congeneric species but also maximize the interspecific traits variability explained variance. At each step, we removed the trait having the smallest contribution in a principal component analysis until we found the smallest distance between species. We retained a combination of six functional traits (Table 1): specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content per unit leaf mass (LNC_{mass}), leaf nitrogen content per unit leaf area (LNC_{area}), seed mass (SM) and wood density (WD: g/cm³). In the PCA, six traits maximized the interspecific traits variability explained (Axis 1:55.8%; Axis 2:29.2%) and minimized the distance between congeneric species and showed that although native/exotic pairs are not perfectly equivalent, they are quite similar relative to

other species (Figure 2). LNC_{area} and LNC_{mass} were highly correlated; however, the distance between congeneric species was smaller when both leaf nitrogen content were kept in the selected traits. Note that the deciduous angiosperm and evergreen gymnosperm species are well distinguished in the trait space and that the two *Larix* species (deciduous gymnosperms) are in-between the deciduous angiosperms and the evergreen gymnosperms in those regards.

Functional diversity was calculated using the functional dispersion index (FDis; Laliberté & Legendre, 2010), defined as the mean distance of each species to the centre of mass of all species in a community in a multidimensional trait space, weighted by the relative abundance of each species. It is noteworthy that various indices of diversity exist and represent different dimensions of the diversity of species. We report results using FDis rather than other diversity indices for several reasons. First, FDis is a multidimensional index that also takes into account species abundances. Second, FDis considers the entire trait space volume of the species pool; thus, the FDis value is relative to that fixed volume and informs on the differences between species. Third, FDis computes for two-species mixtures, contrary to functional richness, functional evenness or functional divergence that require at least three species (Mason et al., 2005; Ricotta et al., 2014). Lastly, FDis gives similar values of diversity to mixtures of functionally equivalent species that differ in provenance, as expected. This experiment was designed to study the effect of the provenance of functionally equivalent species. Theoretically, a mixture of two native species (e.g. a mixture of *Acer saccharum* and *Picea abies*) and a mixture where one of the two species has been substituted for its congeneric exotic equivalent (e.g. *Acer platanoides* and *Picea abies*) should have similar diversity values. In this context, FDis performs particularly well, compared to

FIGURE 2 Principal component analysis on six functional traits used in functional diversity calculations. Arrows represent the functional traits of specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content per unit leaf mass (LNC_{mass}), leaf nitrogen content per unit leaf area (LNC_{area}), seed mass (SM) and wood density (WD). Ellipses represent 75% confidence interval for the native (solid circles and lines) and exotic species (open circles and dashed lines). Dotted lines link the congeneric species differing in provenance. Axis one represents 57.4% of variance and axis two 29.1%. Species abbreviations are reported in Table 1



other diversity indices, by providing diversity values which are very close (and low) for mixtures comprising conspecific, functionally similar species. Consequently, functional diversity, here expressed with FDis, was used as it was seen as the most appropriate diversity index for our experimental design. We used the R function dbFD in the package FD (Laliberté & Legendre, 2010) and the six functional traits previously identified (SLA, LDMC, LNC_{mass} , LNC_{area} , $\log(SM)$ and WD), as well as the abundance of species in each plot at the beginning of the experiment for each species in the two- and six-species mixtures, 0.5 and 0.167, respectively, to calculate the functional dispersion index. Only functional diversity at the beginning of the experiment will be reported since repeating the same analyses with functional diversity every year (to account for mortality and growth rates that differed among species, affecting functional diversity) showed no change in results (Figure S3). We end up with 12 monoculture plots with a functional diversity value of 0 and 36 distinct values of functional diversity for each of the two- and six-species mixtures (Table S1). The R function dbFD also provided community-weighted means (CWM) for each trait used in the calculation. We used the CWM as the functional identity of each plot.

2.4 | Tree productivity

We reported productivity as the species-level basal area per hectare (based on plot area) in each mixture and monoculture. Basal diameter (at 5 cm aboveground) of each individual tree was measured in the fall, for each growing season, from 2010 to 2017 (8th growing season). The yearly basal diameters were then summed by species and by mixture. We obtained the basal area (m^2) of each species related to the plot area which was then transformed into a basal area

per hectare. Thus, each species of each plot has a yearly basal area per hectare (expressed in m^2/ha).

2.5 | Statistical analysis

Linear mixed-effect models were used to investigate the productivity response after 8 years to sites, plot species richness, plot functional diversity, plot functional identity (one functional identity for each of the six traits) and species provenance. We used the *lmer* function in LME4 package (Bates et al., 2015) and LMERTTEST in R (Kuznetsova et al., 2017). Plot species richness was treated as a factor with values of either one, two or six species. Species provenance was considered as a factor (native/exotic). Plot functional diversity and plot functional identity were treated as continuous variables. The plot, genus and species identity were included as random factors since they were not the focus of our investigation. The model used in our study was designed to focus on species-level productivity in each mixture and not on the overall plot productivity (i.e. the sum of all species productivity). Therefore, when we considered a species in a plot, the model referred to the exotic or native provenance of the focal species and not on the provenance of the other species that composed the mixture. We built a full model including two-way interactions between plot functional diversity and site, plot functional diversity and species provenance, and site and every plot functional identity. Since our focus was on the effect of functional diversity and provenance and not on functional identity (that have already been shown and discussed in other BEF studies; Grossman et al., 2017; Tobner et al., 2016), we did not consider the interaction between functional identity and other fixed factors than the site. The best model was selected using *fitLmer.fnc* function in R package

LMERConvenienceFunctions (Tremblay & Ransijn, 2015). This function back-fits the initial model based on ward z-values then forward-fits random effects and re-back-fits fixed effects. The null model, full model and best model were then compared using the *aictab* function in *AICCMODAVG* R package (Mazerolle, 2017; Table 2).

We then applied a post-hoc analysis to the best model, using the R function *emmeans*, to compare levels of the single fixed factors on the response and to test the significance of the single fixed covariates on the response, both functions being in *EMMEANS* package (Lenth et al., 2019). We used the function *emtrends* to compare the slopes of trend lines for the two-way interactions between fixed covariates and fixed factors.

Using the full model, we analysed the effect of the two-way interaction between functional diversity and provenance of species

for each of the 8 years to determine yearly productivity for both sites. For each year, we extracted the slope of the interaction of functional diversity with provenance of the species using *emtrends* function in R package to calculate slopes and compare them.

3 | RESULTS

Productivity was not related to functional diversity alone (Table 3) as we found a significant interaction with provenance. The productivity of North American species was independent of functional diversity (slope = 0.585) while the productivity of European species was positively affected (slope = 4.424; Figure 3a). Plot species richness had a significant positive effect on productivity (Figure 3c). All the other

TABLE 2 Summary of model analysis

Model	Formula	df	AICc	ΔAICc	Log-likelihood
Null model	Productivity ~ random (plot; genus; species)	5	7,370.66	-97.64	-3,680.29
Full model	Productivity ~ Site + SR + FDis + P + FI (SLA; LDMC; LNC _m ; LNC _a ; SM; WD) + P*FDis + Site*FDis + Site*FI (SLA; LDMC; LNC _m ; LNC _a ; SM; WD) + random (plot; genus; species)	24	7,280.75	-7.73	-3,615.64
Best model	Productivity ~ SR + FI (LDMC; LNC _m) + P*FDis + Site*FI (SM) + random (plot; genus; species)	15	7,273.02	0	-3,621.22

SR, Species Richness; FDis, Functional Diversity; P, Species Provenance; FI, Functional Identity; SLA (Specific Leaf Area) mm²/mg; SM (Seed mass; log(g per 1000 seeds)), WD (Wood density; g/cm³), LDMC (Leaf Dry Matter Content; g/g), LNC_{area} (Leaf Nitrogen content per unit area; g/m²), LNC_{mass} (Leaf Nitrogen content per unit mass; mg/g).

TABLE 3 Linear mixed model parameters for the best model

Fixed effects	Estimate	SE	df	t-value	Lower CI	Upper CI	p-values	Partial R ²
(Intercept)	184.85	27.47	79.15	6.73	131.00	238.69	<0.0001	***
Site	1.50	2.17	762.94	0.69	-2.75	5.76	0.489	0.000
FDis	0.59	1.88	30.27	0.31	-3.10	4.27	0.758	0.000
SR - 2	-24.87	3.25	33.61	-7.66	-31.24	-18.51	<0.0001	0.043***
SR - 6	-40.08	4.36	23.25	-9.20	-48.63	-31.54	<0.0001	0.067***
P	1.51	8.06	6.20	0.19	-14.29	17.30	0.858	0.000
FI (SM)	14.34	2.11	83.65	6.81	10.22	18.47	<0.0001	0.039***
FI (LNC _m)	-3.26	0.35	81.16	-9.24	-3.95	-2.57	<0.0001	0.099***
FI (LDMC)	-268.62	69.90	70.07	-3.84	-405.62	-131.63	<0.0001	0.015***
Site: FI (SM)	-4.22	1.55	763.18	-2.72	-7.27	-1.17	0.007	0.004**
P: FDis	3.84	1.80	118.42	2.13	0.31	7.36	0.035	0.003*
Random effects				Variance		SD		
Plot				11.73		3.43		
Species				169.70		13.03		
Genus				238.16		15.43		
Residual				298.81		17.29		
R ² conditional				0.68				
R ² marginal				0.23				

SR, Species Richness; FDis, Functional Diversity; P, Species Provenance; FI, Functional Identity; SLA (Specific Leaf Area) mm²/mg; SM (Seed mass; log(g per 1000 seeds)), WD (Wood density; g/cm³), LDMC (Leaf Dry Matter Content; g/g), LNC_{area} (Leaf Nitrogen content per unit area; g/m²), LNC_{mass} (Leaf Nitrogen content per unit mass; mg/g). **p* < 0.05, ***p* < 0.01; ****p* < 0.001.

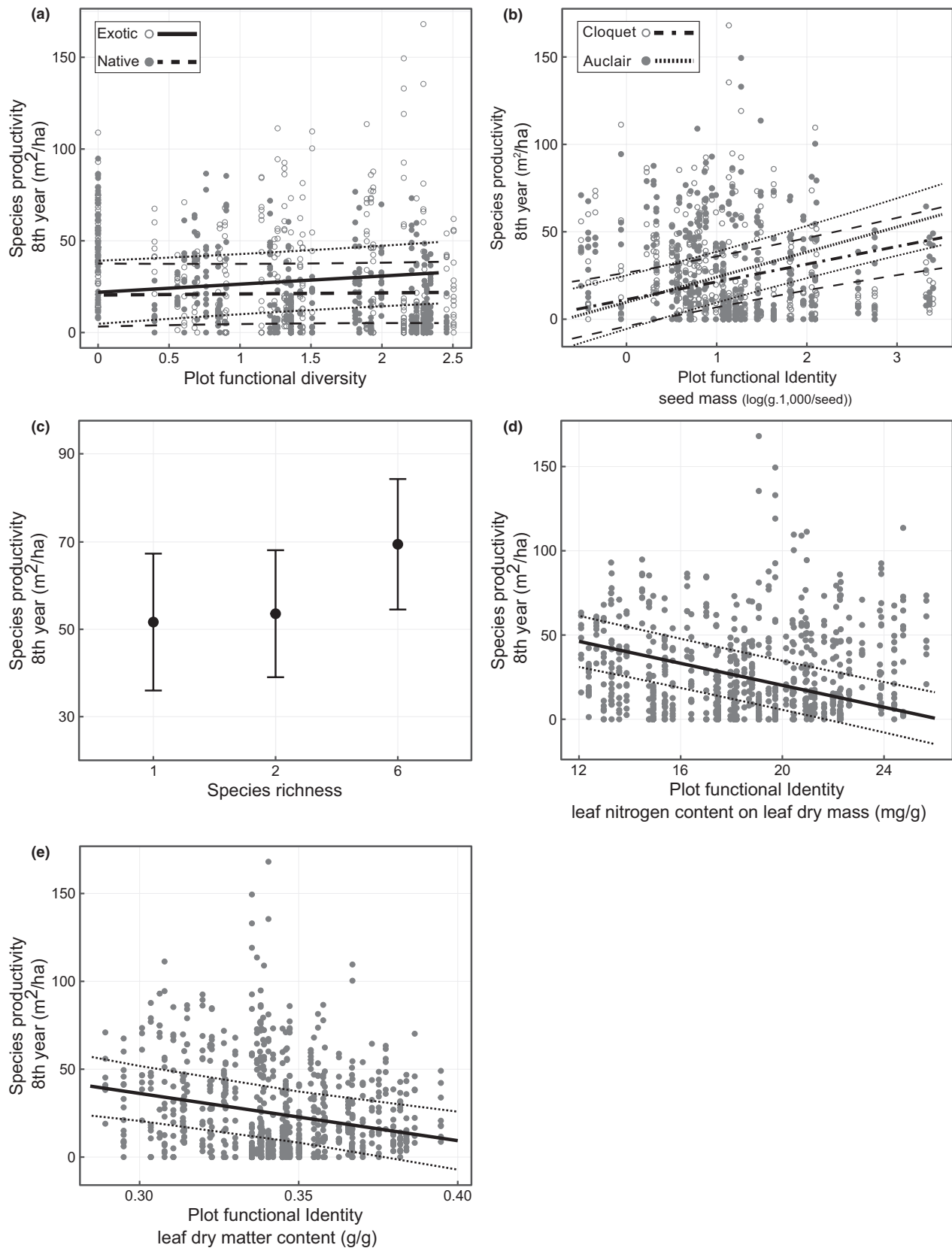


FIGURE 3 Effects on productivity over 8 years. Details of the significant single and two-way interaction fixed effects are reported in Table 3. (Panel a) Functional diversity and species provenance; (Panel b) functional identity of seed mass and site (the single effect of functional identity of seed mass is involved in two interactions and is therefore not shown); (Panel c) species richness; (Panel d) functional identity of leaf nitrogen content; (Panel e) functional identity of leaf dry matter content. Points represent each species productivity per plot and block. Error bars represent the 95% confidence intervals of the effect

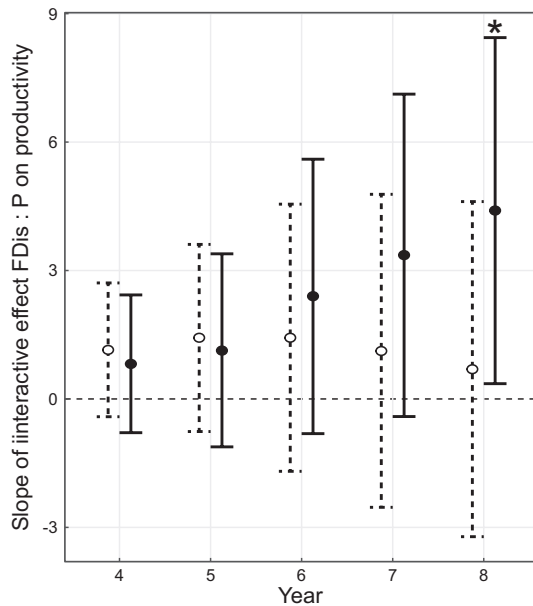


FIGURE 4 Estimates of the interactive effect of functional diversity with species provenance on annual productivity over time. Significant differences among provenances start at the eighth year. The seventh year presents a marginally significant difference between native (dotted bars) and exotic species (plain bars). Estimates are calculated using the full model. Error bars represent the 95% confidence intervals of the effect. * $p < 0.05$

significant effects involve functional identity in two-way interactions or single fixed effects. Productivity decreased with leaf nitrogen content and leaf dry matter content (Figure 3d–e). Productivity increased with seed mass at both Auclair and Cloquet, being slightly higher at Cloquet (Figure 3b; $p = 0.0068$, $df = 784$, Tukey test). The model presented in Table 3 was significantly better than the full model ($\Delta AICc = -7.73$) and the null model ($\Delta AICc = -97.60$; Table 2). The same analysis performed with FDis calculated on the abundances and SR of the eighth year gave similar results (Table S2).

The strength of the functional diversity effect and the difference between species increased over time (Figure 4). Starting from year 7, native and exotic species tended to diverge in the strength of their effect. The seventh year presents a marginal significant difference between native and exotic species ($p = 0.171$, $df = 189$, Tukey test). The difference in slope was significant only in the eighth year ($p = 0.046$, $df = 163$, Tukey test). Functional diversity effect for European species was positive and stronger every year starting from the fifth year. The effect of functional diversity on North American species was slightly positive in the fifth year, stabilized during the sixth year, then decreased to become null again.

4 | DISCUSSION

The trait-based ecology framework is based on the hypothesis that species functional performance can be described using a quantitative measurement of morphological, physiological or phenological attributes at the cell, tissue, organ or individual level. The argument

is that these plant attributes are related to individual performance (growth, reproduction and survival) in a given environment, which determines the performance of species in that environment (Garnier et al., 2016; Reich, 2014; Violle et al., 2007). The functional trait approach also suggests that two species showing similar trait values should play equivalent roles, resulting in similar interactions and performances in a similar environment. In this study, we challenge the trait-based ecology framework (or more specifically that it alone cannot explain all responses) by comparing exotic and native species showing similar functional trait values but varying in their geographical provenances.

According to this hypothesis, an exotic species and a native species with similar functional trait values should be interchangeable without causing much variation in the functioning of an ecosystem. *Betula pendula* and *B. papyrifera* for instance are two deciduous pioneer species with very similar trait values (Figure 2) but originate from Europe and North America, respectively. In a biodiversity–ecosystem functioning context, substituting a native species (*B. papyrifera*) for its congeneric exotic species (*B. pendula*) in a mixture should not change the functional diversity of the mixture nor its productivity. That said, the two species can be similar in their resource-use functional traits values but can differ in other traits related to life history, including defence against enemies, time to maturity or mortality, which might influence performance in mixtures. The two *Betula* species showed relatively similar productivities in monoculture (Figure S4); however, when both species were in mixture with *Acer platanoides*, *Betula pendula* was more productive than *Betula papyrifera*. Another example could be the pair *Picea abies* and *Picea glauca* that had relatively similar productivity in monoculture and in mixture with a functionally close species *Pinus strobus*. However, in mixture with a functionally distant species *Acer saccharum*, the exotic species *Picea abies* is more productive than its native congener.

4.1 | Positive effect of functional diversity on productivity

Our results confirm that productivity increases with increasing species richness and functional diversity in different mixtures, when considered independently (Figure 3a). Very few studies to date have investigated both diversity indices (Paquette & Messier, 2011; Van de Peer, Verheyen, et al., 2018). Our results are consistent with Van de Peer, Verheyen, et al. (2018) showing that functional diversity is a stronger driver than species richness in explaining productivity. Likewise, Paquette and Messier (2011) demonstrated through structural equation modelling that functional diversity was a direct predictor of tree productivity while species richness had an indirect effect (through FDis). Some prior studies have also shown the positive effect of diversity, at local and large scales, but mostly only considered species richness (Balvanera et al., 2006; Cardinale et al., 2007; Hooper et al., 2005; Jactel et al., 2018; Liang et al., 2016). Other studies have shown a positive effect at a local scale related to crown complementarity (Pretzsch et al., 2015; Williams et al., 2017),

nutrient cycling complementarity (Reich et al., 2012), seedling vitality (Van de Peer, Mereu, et al., 2018) or multifunctional level of the mixtures (Van der Plas et al., 2016). However, our results also showed a high variability in responses of the mixture to diversity (Figure S4). This variability suggests that the composition of mixtures plays a part in the diversity–productivity relationship. Indeed, in the study by Van der Plas (2019), as well as in the present experiment, functional diversity had positive effects on productivity more often than negative effects, but some mixtures clearly showed a negative effect. Overall, our results do not support the negative effect of species richness reported in several other studies in natural herbaceous communities (Thompson et al., 2005), semi-natural settings (Sandau et al., 2019) or controlled experiments (Haase et al., 2015).

4.2 | Effect of geographical origin on the diversity–productivity relationship

We found that the positive effect of functional diversity on productivity increased over time for the exotic species and significance reached $p < 0.05$ in the final year of the experiment, whereas there was no effect on productivity for the native species (Figure 3a). Productivity of monocultures was, on average, independent of provenance ($F_{Dis} = 0$), indicating that when growing alone, native species were as productive as their exotic counterparts. In monoculture, species are solely in intraspecific competition, while in mixture, species experience intraspecific and interspecific competition. In mixtures, the differences between native and exotic species increased over time, due to differences in their interspecific interactions, with some species showing a positive effect and others experiencing negative effects (Figure S4). Productivity is only increasing for exotic species in combination of mixtures where exotic grew with native species. All the other combinations expressed either a neutral or a negative effect on productivity due to strong negative interactions. This suggests that, on average, native species suffered from interspecific competition with both native and exotic species (as compared with intraspecific competition), whereas exotic species suffered from interspecific competition with exotic species but benefited from competition with native species (as compared with intraspecific competition).

4.3 | Trophic complementarity explaining the effect of functional diversity and provenance of species

The difference in productivity over time due to the provenance of species is consistent with the enemy release hypothesis affecting apparent competition and trophic complementarity between species (Poisot et al., 2013; Figure 4). We investigated whether exotic species were more productive and complementary than native species by comparing the F_{Dis} –productivity relationships. In mixtures, exotic species reacted positively to an increase in functional diversity

while native species did not react to diversity. Consistently with our findings, Wilsey et al. (2009) also showed that exotic species, in grasslands, benefit more than native species from being mixed with functionally different species. In our study, this was evidenced by the similar productivity of native and exotic species during the first few years of the experiment (Figure 4). However, as time went on, differences between native and exotic species became more pronounced. These differences were not related to a specific functional trait (or functional identity; Figure 4). Although native and exotics congeners were not exactly similar in their traits make-up (Figure 2), they were nonetheless quite close to each other relative to the other species considered. The observed differences in their productivity therefore suggest there are some other aspects of the species biology relevant to their performance that is not related to the resource-use functional traits we considered. One possibility is that we missed relevant resource-use functional traits, or alternatively that native and exotic differ in their interactions with enemies and allies at all trophic levels.

Trees interact with several trophic levels. Native species interact with consumers but also with co-adapted mycorrhiza and other soil and leaf microbes (Laforest-Lapointe et al., 2017; Tedersoo et al., 2020); we can only speculate that it should be more difficult for exotic species to interact with specialist mycorrhiza and microbes; moreover when such relationships are mutualistic, such difficulties would lead to poorer performance of exotics, which was not observed in such mixtures. Mycorrhizal and leaf or soil microbial communities can also interact with plant species and positively or negatively affect their productivity due to the release of ‘enemies’ pressure (Agrawal et al., 2007; Mitchell & Power, 2003). In the same way, an exotic tree may be less affected than native species by a local pest, as is the case for *Acer saccharum* and *A. platanoides* (Adams et al., 2009; Cincotta et al., 2009).

Furthermore, a recent assessment across continents provided evidence that escape and release from herbivores facilitated the invasion of *A. platanoides* as leaf damage was consistently lower in its novel range compared to its native range (Adams et al., 2009). The same type of study was conducted at the IDENT site in Freiburg, Germany (identical to IDENT AuCI), and no difference in herbivory was found between native and exotic congeneric species (Wein et al., 2016). Yet, the authors stated that the prevalent herbivores were probably generalists and consequently caused similar damage to both the exotic trees and the neighbouring native congeners. However, several studies have shown that specialist insect herbivores in native species can switch to their exotic congeners over time and mitigate the effect of the generalist herbivores (Keane & Crawley, 2002).

Microbial and mycorrhizal interactions may also differ between native and exotics. Yang et al. (2013) found that a Chinese species, *Triadica* sp, imported into the United States had greater productivity due to soil biota and mycorrhizae in its soil. They explained that differences in biomass were due to a ‘home’ soil already containing pathogens specific to native species and few or no pathogens that could affect exotic species. In contrast, the study by Nguyen

et al. (2016) at the Cloquet IDENT site showed a positive relationship between plant diversity and ectomycorrhizal fungal richness. The effect of provenance of species was attributable to differences in community heterogeneity in resources and micro-environmental conditions. In another experiment with springtail at AuCI, Raymond-Léonard et al. (2018) showed that biogeographical origin of the leaf litter did not significantly influence springtail community structure. They suggested that species leaf traits, more than their biogeographical origin, affected the springtail communities.

4.4 | Effect of time on the productivity–diversity relationship

We found that the differences in the functional diversity–ecosystem functioning relationship between provenances increased over time (Figure 4). Similar observations were also reported in several studies in grasslands (Cardinale et al., 2007; Cook-Patton & Agrawal, 2014; Reich et al., 2012) where the complementarity effect grew stronger over time. However, until now, this had not been shown in tree experiments with native and exotic species. It is interesting to note that during the fourth and fifth years, both native and exotic species displayed the same slightly positive effect of diversity. This variation shows that, at least during the initial years, interspecific interactions did not impact productivity sufficiently to be detected but this impact built up over time. Most likely due to the high density in the experiment, it took 8 years for exotic species to show a significant difference. Interestingly, we also found increasing confidence intervals for the slopes over time. This result is likely due to an increase in mortality in the plots that led to fewer but larger trees (not shown).

5 | CONCLUSIONS

In this experiment, we tested the effect of the provenance of species on tree community productivity. Our results show a general positive effect of functional diversity on species productivity. However, this effect was positive for exotic tree species and null to modestly positive for native species. In addition, this effect was not present in the first few years of the experiment, became more evident with time and reached significance in the last year. After 8 years, exotic species were more productive overall than their similar native counterparts but only in more functionally diverse communities. Although we did not measure the interactions between the exotic tree species and their local 'enemies', our results are consistent with the hypothesis of a change in trophic complementarity and apparent competition between native and exotic species. Confirmation of this hypothesis will require measurements of the effect of herbivores and microbes on both native and exotic species as well as measurements of the soil microbial allies and enemies over several consecutive years. This study represents a first step in understanding the relative importance of resource and trophic complementarity with the introduction of exotic tree species.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.P., D.G., C.M. and P.B.R. conceived the ideas and designed the methodology; A.P., D.G., C.M., A.S. and P.B.R. collected the data; M.B. and D.G. analysed the data; M.B. and D.G. led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.m0cfxpp4h> (Belluau et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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