Received: 7 September 2022 | Revised: 2 March 2023 | Accepted: 14 March 2023

DOI: 10.1002/ecy.4070

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Exotic tree species have consistently lower herbivore load in a cross-Atlantic tree biodiversity experiment

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Funding information
Baden-Württemberg Stiftung, Grant/Award Number: 1.16101.17; National Science Foundation, Grant/Award Number: NSF-DBI-2021898; Natural Sciences and Engineering Research Council of Canada Discovery grant

Handling Editor: Matthew L. Forister

Abstract

It is commonly expected that exotic plants experience reduced herbivory, but experimental evidence for such enemy release is still controversial. One reason for conflicting results might be that community context has rarely been accounted for, although the surrounding plant diversity may moderate enemy release. Here, we tested the effects of focal tree origin and surrounding tree diversity on herbivore abundance and leaf damage in a cross-Atlantic tree-diversity experiment in Canada and Germany. We evaluated six European tree species paired with six North American congeners in both their native and exotic range, expecting lower herbivory for the exotic tree species in each pair at each site. Such reciprocal experiments have long been called for, but have not been realized thus far. In addition to a thorough evaluation of overall enemy release effects, we tested whether enemy release effects changed with the surrounding tree diversity. Herbivore abundance was indeed consistently lower on exotics across all six tree genera (12 comparisons). This effect of exotic status was independent of the continent, phylogenetic relatedness, and surrounding tree diversity. In contrast, leaf damage associated with generalist leaf chewers was consistently higher on North American tree species. Interestingly, several species of European weevils were the most abundant leaf chewers on both continents and the dominant herbivores at the Canadian site. Thus, most observed leaf damage is likely to reflect the effect of generalist herbivores that feed heavily on plant species with which they have not evolved. At the German site, sap suckers were the dominant herbivores and showed a pattern consistent with enemy release. Taken together, the consistently lower herbivory on exotics on both continents is not purely a pattern of enemy release in the strictest sense, but to some degree additionally reflects the susceptibility of native plants to invasive herbivores. In conclusion, our cross-Atlantic study is consistent with the idea that nonnative trees have generally reduced herbivory, regardless of tree community diversity and species identity, but for different reasons depending on the dominant herbivore guild.

KEYWORDS
arthropods, associational effects, enemy release, exotic, herbivores, herbivory, IDENT, insects, native, tree diversity

INTRODUCTION

Exotic species may experience a release from natural enemies (e.g., predators, herbivores or pathogens) in their introduced range (Heger & Jeschke, 2014). Such "enemy release" (ER) has been most commonly investigated in invasion biology, in which the "enemy release hypothesis" (ERH) tries to explain the success of invasive exotic species (Enders et al., 2020). The ERH not only requires an exotic species to experience ER, but also that leads to increased performance in the new range and hence facilitates invasion (Heger & Jeschke, 2014). The wealth of studies investigating the ERH has found only mixed support (Ashton & Lerdau, 2008; Chun et al., 2010; Colautti et al., 2004; Heger & Jeschke, 2014). Here, we focus on whether exotic plant species experience reduced herbivory in terms of herbivore load or damage, the aspect of the ERH that arguably has received the most attention so far (Keane & Crawley, 2002; Liu & Stiling, 2006; van Kleunen et al., 2015). Whereas many previous studies have considered herbaceous plants, here we evaluate ER for trees. Also, almost all previous studies have either compared species in their native range to the introduced range (biogeographical approach), or compared exotic species with co-occurring native species (community approach), with very few exceptions embracing both comparisons (Meijer et al., 2015; Norghauer et al., 2011). In the meta-analysis of Colautti et al. (2004), evidence for ER was clear for the biogeographical approach, but very limited for the community approach, while other meta-analyses have found some support with both approaches (Liu & Stiling, 2006; Meijer et al., 2016). However, each of these two approaches alone is prone to confound exotic status with effects of sites or species identity, which can only be avoided by fully crossing the two approaches. This means using parallel common gardens in the native and introduced range, that is, comparing each species both in its native and in its exotic range to the same set of other species that are native where the focal species is exotic. Although such a systematic combined approach has already been called for by Colautti et al. (2004), to our knowledge, such an approach has so far not been implemented.

ER has mostly been studied for plant species in isolation, disregarding the influence of surrounding plant diversity. One exception is a comparison of oak herbivory among North American arboreta that found more ER in regions with lower oak diversity (Pearse & Hipp, 2014). Exotic plants can be found in a variety of communities, ranging in diversity from those dominated by a single invasive species to novel communities that represent mixtures of native and nonnative plants (Bezemer et al., 2014; Hobbs et al., 2006; Tallamy, 2004). In mixed plant communities, herbivory on a focal plant can be influenced by neighboring plant species (Barbosa et al., 2009; Underwood et al., 2014), for example due to the lower density or frequency of a focal species in a diverse community. For example, Root (1973) proposed the "resource concentration hypothesis," which states that specialist herbivores attain higher densities in pure stands of host plants. "Associational effects" in the stricter sense are those driven by neighbor identity or diversity (Underwood et al., 2014). Neighbors may reduce herbivory on a focal plant ("associational resistance [AR]"). AR may add up at the community level such that herbivory decreases with increasing plant diversity (Grossman et al., 2019). With the rise of biodiversity–ecosystem functioning (BEF) research, the effects of tree diversity on herbivory have now been evaluated in multiple experiments. These have shown that tree diversity often reduces herbivory (Jactel et al., 2021), but the opposite (tree diversity increases herbivory) is also not uncommon (Wein et al., 2016). Very few tree-diversity experiments have included comparisons of native and exotic trees (Berthelot et al., 2021; Schuldt & Scherer-Lorenzen, 2014; Wein et al., 2016), and none of these have identified how tree diversity mediates ER from herbivores.

Some variation in observed ER effects may be explained by differences between specialist and generalist herbivores: ER particularly concerns the absence of specialist herbivores in the introduced range, although attack by generalist herbivores may also be reduced on exotic species (Keane & Crawley, 2002). Meta-analyses have not provided a definite answer regarding the importance of herbivore specialization for ER (Heger & Jeschke, 2014). Generalists might attack exotic species less (due to their novelty or due to shifted defenses: Joshi & Vrieling, 2005), equally, or more than native trees (if exotics lack defenses against these herbivores: Parker et al., 2006). Even specialized herbivores often attack multiple plant species of the same plant genus or family (Ali & Agrawal, 2012), thus ER may not occur for closely related species, whereas exotic species that are phylogenetically isolated from natives may experience the greatest ER (Hill & Kotanen, 2009; Pearse & Hipp, 2014; Tallamy, 2004).

The degree of herbivore specialization is a major structuring concept not only for expectations about ER, but also for expectations about associational and tree-diversity effects. AR is derived from the assumption of high herbivore specialization and may not apply to generalists. Generalist herbivores may spill over between neighbor plants, reducing the scope for AR (and negative tree-diversity effects on herbivory) and increasing the scope for "associational susceptibility" (AS), and positive tree-diversity effects on herbivory, for example, due to resource complementarity being provided by multiple plant species. Research has generally confirmed that tree-diversity effects on specialist herbivores tend to be more negative than for generalists (Grossman et al., 2019; Jactel & Brockerhoff, 2007; Koricheva et al., 2006).

Against this background, we can derive the following predictions regarding how tree diversity in the community mediates ER. For generalist herbivores, ER is moderate and disappears with increasing tree diversity (due to AS), that is, herbivory on exotic species will be higher in mixed than in pure stands. For specialist herbivores, ER is strong but weakens with increasing diversity (due to AR), that is, herbivory on native species will be lower in mixed compared with pure stands. This leads us to expect that ER effects for all herbivores combined will be strongest in pure stands and may vanish in mixed stands.

Here, we studied the effect of tree origin (native vs. exotic) and its interaction with neighbor tree diversity (richness) on herbivory (herbivore abundance and leaf damage). We used a unique cross-Atlantic tree-diversity experiment (IDENT) with congeneric pairs of North American and European trees to tease apart tree species identity from native versus exotic origin. As the IDENT sites in Freiburg, Germany (Wein et al., 2016), and Auclair, Canada (Tobner et al., 2014) had the same set of tree species and study design, we could evaluate the effects for 12 tree species in six genera (three conifers, three broadleaves). We first tested the hypothesis (H1) that the difference between congeneric pairs of tree species is inverted between sites, with lower herbivory for the exotic species on each continent (ER). We evaluated herbivore specialization and tree phylogeny as potential moderators of H1, with subhypotheses (H1a) that herbivore guilds that tend to be specialists show the strongest ER and (H1b) that exotic tree species closely related to the native congener show the weakest ER. Second, we tested hypothesis (H2) that the strength of ER depends on the community context (neighborhood tree diversity) and origin effects are less pronounced in mixtures than monocultures. For H2, we evaluated the subhypothesis (H2a) that tree diversity reduces herbivory only for herbivore guilds that tend to be specialists. Examining herbivory on native and exotic tree species in this full-factorial experiment makes our study one of the strongest tests of enemy release so far, isolating the exotic status per se from other confounders.

METHODS

Study sites

The study was conducted at field sites in Auclair, Québec, Canada, and Freiburg, Germany, which are part of IDENT, the International Diversity Experiment Network with Trees (Tobner et al., 2014). IDENT-Auclair is located in southeastern Canada (47°41′47″ N, 68°39′22″ W; 333 m above sea level [asl]). The soil is loamy and the study site is bordered by grass fields and mixed forest. IDENT-Freiburg is located in southwestern Germany (48°01′10″ N, 7°49′37″ E; 240 m asl). The soil is sandy–loamy and the study site is surrounded by grassland in the immediate vicinity, with residential areas and a broadleaved forest at ~100 m distance.

Experimental design

IDENT-Auclair was planted with ~10,000 tree seedlings in plots of 7 rows × 7 columns of trees at a distance of 40 cm (49 trees per plot; plot area 10.2 m^2) in 2010.

A buffer of 1.4 m separated adjacent plots. For detailed planting information see Tobner et al. (2014). IDENT-Freiburg was planted in 2013 with ~20,000 tree seedlings in plots with 7 × 7 trees at a distance of 45 cm (49 trees per plot; plot area 13 m^2) and a buffer of 1.8 m between plots. For detailed planting information see Wein et al. (2016).

The tree species pool of both sites consisted of 12 species selected according to functional traits and the continent of origin. Six species originate from North America and six from Europe, with three gymnosperm (conifer) and three angiosperm (broadleaf) species from each continent (Tobner et al., 2014; Wein et al., 2016). Species belong to six genera, which results in congeneric pairs of a European (mentioned first) and a North American (mentioned second) representative: *Acer platanoides* L., *A. saccharum* Marshall, *Betula pendula* Roth, *B. papyrifera* Marshall, *Quercus robur* L., *Q. rubra* L., *Larix decidua* Mill., *L. laricina* (Du Roi) K. Koch, *Picea abies* (L.) H. Karst., *P. glauca* (Moench) Voss, *Pinus sylvestris* L. and *P. strobus* L. In Freiburg, *Picea glauca* was ordered but the closely related North American *Picea pungens* (var. *glauca*) Engelm. was erroneously supplied by the nursery and thus planted. Both North American *Picea* species were treated conceptually as one functional species in this study. Of all planted species, only two are naturalized widely in the exotic region, being introduced presumably within the last 250 years: *Quercus rubra* is not considered invasive in Germany (Vor et al., 2015), but occurs in forests close to the Freiburg site. *Acer platanoides* is considered invasive in North America (Adams et al., 2009; Cincotta et al., 2009), but is not known to occur in forests close to the Auclair site. The other species may also be present in the exotic range, for example, in arboreta, but rarely occur in forests.

In both Auclair and Freiburg, the experimental design includes four blocks. In Auclair, 12 monocultures (one of each species), 30 plots with two-species mixtures and six plots with six-species mixtures were planted per block, resulting in a total of 192 plots. In Freiburg, plots with matching mixtures were used, resulting in a total of 172 plots (as there are only 25 different two-species mixtures in Freiburg). Plots had either 100% native, 50 : 50% native : exotic, or 100% exotic species planted, with the proportion of exotics being balanced over the tree-diversity gradient (see Appendix S1: Table S1 for more details on the composition of the mixtures). Positions of plots in blocks were randomized but identical mixtures were not allowed to be direct neighbors.

Arthropod sampling and sorting

Arthropod abundance was monitored on 1144 trees in Auclair, Canada and 827 trees in Freiburg, Germany in two sampling rounds. Arthropod sampling with beat sheets was conducted between 21 May and 6 June 2018 as well as 20 June to 3 July 2018 in Auclair, and 8 April to 29 April 2019 as well as 11 June to 28 June 2019 in Freiburg, with the onset of sampling in the first-round coinciding with budbreak (earliest were *Betula* and *Larix* spp.). The second round of sampling was conducted when canopies of all species were fully developed. Arthropods were sampled on six trees per plot in the core area of each plot consisting of 5 × 5 trees. Trees were selected randomly, selecting three trees per species in two-species mixtures and one tree per species in six-species mixtures. A customized circular beat sheet measuring 40 cm in diameter and a 2-m-long stick were used for beating. Trees <1 m in height were sampled once, whereas trees >1 m were sampled once at the bottom of the crown and once in the middle of the crown. For sampling portions of the crown at heights >2 m, a telescopic rod was used to lift the beat sheet. Trees with short branches (<30 cm) and trees with crowns starting at >3 m were shaken once instead of beaten. Collected arthropods were stored in 70% ethanol until identification in the laboratory.

Arthropods were sorted into feeding guilds based on order, suborder, or family-level identification using a stereomicroscope. Representatives of commonly found herbivore taxa were further identified to the species level using specialized literature or DNA barcoding (Appendix S1: Table S2). We defined guilds that differed in average specialization (Novotny et al., 2010). The following groups were classified as sap-sucking herbivores (or suckers, for simplicity): Sternorrhyncha (order Hemiptera), Auchenorrhyncha (order Hemiptera) and many Heteroptera (order Hemiptera; families Acanthosomatidae, Miridae, Lygaeidae, and Pentatomidae). Chewing (incl. skeletonizing) herbivores were split into adult and larval chewers, as these may have shown marked differences in average specialization (Forister et al., 2015). Weevils (Coleoptera: Curculionidae; mainly subfamily Entiminae) and leaf beetles (Coleoptera: Chrysomelidae) were classified as adult chewers. Caterpillars (order Lepidoptera) and sawfly larvae (Hymenoptera: Tenthredinoidea) were classified as larval chewers. Based on the literature (Ali & Agrawal, 2012; Forister et al., 2015; Novotny et al., 2010), among the free-living herbivore guilds we consider suckers and larval chewers to be more specialized on average than adult chewers. The orders Araneae, Opiliones, Dermaptera, Neuroptera (larvae), as well as the families Coccinellidae (order Coleoptera) and Nabidae and Reduviidae (Hemiptera: Heteroptera) were classified as predators. The remaining arthropods were classified as "others." Here we focus on herbivores, but results for predators and "others" are presented in Appendix S1: Tables S3 and S4. Overall herbivore abundance data, as well as guild-specific abundance data from the two sampling rounds, were summed for analyses.

Leaf damage

In Auclair, leaf damage was assessed on trees sampled with the beat sheet for all plots in blocks 1 and 4, and for monoculture plus six-species-mixture plots in blocks 2 and 3 (786 trees; two-species mixtures in blocks 2 and 3 were not sampled due to time constraints) in July 2018. In Freiburg, leaf damage was assessed on all trees (1243 trees) that had been subjected to beat-sheet sampling in July 2019, when crowns were fully foliated. On each tree, 10 leaves on the lower part of the crown (the lowest one-third of the crown; five leaves at the tip of a branch and five leaves at the base of the same branch) plus 10 leaves between the middle and top of the crown (highest two-thirds of the crown; same branch-level sampling as for lower crown) were monitored. Leaf damage was classified into chewer, miner, skeletonizer, roller, and gall damage, estimating the percentage of missing leaf area (Johnson et al., 2016). In total, 40,580 leaves and needle shoots were assessed for leaf damage. Sap-sucker (e.g., aphids) damage could not be reliably quantified by visual inspection and was thus excluded from analyses. For analyses, leaf damage was summed over all damage types and averaged over all leaves assessed for a given tree.

Data analyses

All analyses were performed in R version 4.03 (R Core Team, 2020). We analyzed the data at the level of tree individuals using mixed effects models, with separate models for herbivore abundance and for leaf damage as response variables. Arthropod abundance data were analyzed using a negative binomial generalized linear mixed model (GLMM) (R package *glmmTMB*: Brooks et al., 2017; family nbinom2) and leaf damage data were analyzed with a linear mixed model (LMM) (R package *lme4*: Bates et al., 2015, R package *lmerTest*: Kuznetsova et al., 2017; mean leaf damage per tree was $\log(y+1)$ transformed prior to analysis). All models contained a random effect of plot. Model structures were based on experimental design and hypotheses. This means we used a different model structure for hypotheses H1 and H2, but did not perform any model selection (e.g., did not remove nonsignificant interactions), apart from the necessary addition of interactions led by model diagnostics (see below).

We evaluated H1 by fitting the fixed effects of site (Europe vs. North America), tree genus, and status (being native or exotic at a given site) and all their interactions. This model was used to show the degree of consistency of enemy release effects across sites and tree genera, allowing us to assess all comparisons of native and exotic congeners at each site. However, testing overall effects (independent of species and site) was difficult with this model structure, which was therefore changed for H2.

For H2, we simplified the fixed effects component in order to explicitly test the main hypothesis of interest, namely the interaction between native/exotic status of the focal tree and the diversity of the tree community. Thus, we fitted a fixed effect of site, native/exotic status, and tree species richness, plus the interaction between native/exotic status and tree species richness. We log transformed the predictor tree species richness. The variability of effects among species was modeled by including a random effect of tree species (random slope approach: status effect and intercept varying among species) in addition to the random intercept of plot. With this model structure, the significance of the main interaction could be assessed as a single-parameter test.

Subhypotheses H1a and H2a (effects depend on herbivore specialization) were assessed by fitting separate models for the abundance of each main herbivore guild (sucker, adult chewer and larval chewer) and comparing the models between the different response variables. Subhypothesis H1b (enemy release effects increase with phylogenetic isolation) was evaluated by modifying the fixed effects structure of the H1 model for herbivore abundance, our main response variable. We removed "genus" from the fixed effects and instead used the following fixed effects predictors: tree status (native vs. exotic), square-root(phylogenetic distance), site, the interaction between site and tree status, and the interaction between square-root (phylogenetic distance) and tree status. The interaction between phylogenetic distance and tree status assesses subhypothesis H1b. Intrageneric phylogenetic distances (i.e., the distance between the pair of congeners) were based on a dated phylogeny of the IDENT tree species (Christophe, 2020) and calculated as cophenetic distance using R package *ape* (Paradis & Schliep, 2019). The intrageneric phylogenetic distance was the largest for gymnosperms (Appendix S1: Table S5). Although the two North American spruce species (*P. glauca* and the erroneously supplied *P. pungens* var. *glauca*) were treated as one functional species in other analyses, they were treated as different species when calculating phylogenetic distance.

In addition, to check if herbivore abundance explained the leaf damage, the structure of the H1 model for chewer abundance was used, but fixed effects predictors were replaced by chewer abundance in the interaction with site. Here, abundance and damage variables were defined to match most closely to each other (only broadleaves, summing adult and larval chewers as "chewer abundance" and summing chewer and skeletonizer damage as "chewer damage").

Arthropod abundance as quantified here is essentially a measure of density (individuals per crown volume). When arthropod abundance was extrapolated to whole trees (by accounting for the approximate proportion of the crown covered by sampling), the results were qualitatively identical.

Model diagnostics were performed with dharma (Hartig, 2021), focusing on the visual inspection of diagnostic plots based on simulated residuals. These showed that model assumptions about residual distributions were reasonably met for abundance models. For initial leaf damage models, however, diagnostics were unacceptable (strongly curved Q–Q plot and extremely low variance of residuals for low predicted values). We therefore restricted the leaf damage analysis to broadleaved trees, given that damage on conifer needle shoots was very rare (87% of conifer trees had no signs of damage on the sampled shoots). The resulting model was acceptable for H1, but the H2 model still indicated poor distributional fit (strong pattern in plot of residuals vs. predicted values, indicating that effects differed between sites). We hence added the two-way interactions with site (tree status by site and tree species richness by site) as fixed effects to the H2 model, which resolved the issue with the poor distributional fit. Adding these by-site interactions also to the abundance models (where they were not significant, $p > 0.1$) did not change results qualitatively. Effect plots (marginal predictions) were created using R package *ggeffects* (Lüdecke, 2018).

RESULTS

In total, nearly 13,000 arthropods were sampled. The majority of these were herbivores, of which the most abundant families were weevils in Auclair and aphids in Freiburg (Appendix S1: Table S2). Further inspection of common taxa confirmed that our guild classification aligned with clear differences in average specialization: Broad-nosed weevils of the genera *Phyllobius* (e.g., *Ph. oblongus*) and *Polydrusus* (e.g., *Po. sericeus*), which are polyphagous and native to Europe (Pinski et al., 2005a; Vollmann, 1954), contributed the largest share to the adult-chewer guild. In contrast, the sap-sucker guild contained many monophagous or oligophagous aphid species, such as *Euceraphis* spp. on *Betula*, *Periphyllus* spp. on *Acer*, *Schizolachnus* spp. on *Pinus*, as well as other specialized Sternorrhyncha and Auchenorrhyncha, in addition to some polyphagous plant-hoppers such as *Issus coleoptratus*. The larval chewer guild (mostly Lepidoptera) was present only in low numbers at both sites and is thus reported only in Supporting Information (Appendix S1: Tables S3 and S4, Figure S1). Guild composition differed markedly between sites, with adult chewers being dominant in Auclair and sap suckers being dominant in Freiburg. The observed leaf damage was primarily chewing damage (97.5% of damage). Damage by more specialized herbivore guilds was too rare to analyze (<0.2% of leaves with miners, rollers, or galls, although these were mostly found on natives; Appendix S1: Table S6).

H1 Are congeneric differences inverted between sites, indicating consistent effects of exotic status?

A lower abundance of herbivorous insects was found on exotic compared with on native trees (Figure 1, Table 1), on both continents and across all six genera. This was true for all herbivores combined (Figures 1a and 2) as well as for the sap-sucker (Figure 1b) and adult leaf-chewer guilds considered separately (Figure 1c). However, the strength of the effect of exotic status on herbivore abundance (total or per guild) varied among tree genera, indicated by a significant interaction between tree status and genus (all $p < 0.01$; see Table 1 for test statistics and additional details for this and other results reported in the following paragraphs). Exotic status effects were small for maple (*Acer*) and oak (*Quercus*), and much larger (up to five-fold higher mean abundance on native species compared with its exotic congener) for birch (*Betula*), larch (*Larix*) and pine (*Pinus*).

For herbivore guilds considered separately, the pattern was influenced by low sap-sucker abundance in Auclair and low adult-chewer abundance in Freiburg. Nevertheless, there was no significant interaction between site and status (except for a three-way interaction suggesting that effects on sap-sucker abundance varied among tree genera depending on the site). Whenever adult-chewer abundance clearly differed between native and exotic congener, it was higher on the native.

Leaf damage (on broadleaves) was, on average, higher on natives than exotic congeners (Figure 1d), but there was a clear difference between sites ($p < 0.001$ for site by status interaction; Table 1): in Auclair, all three natives had more damage than exotic congeners (one-third to three times higher, with mean damage on natives of between 7% and 8.5%), whereas in Freiburg exotics had slightly more damage than their native congeners (up to two-thirds higher, with mean damage on all species of less than 5%). Chewer abundance (adult + larval chewers) corresponded well to chewing damage (including skeletonizing) for Auclair

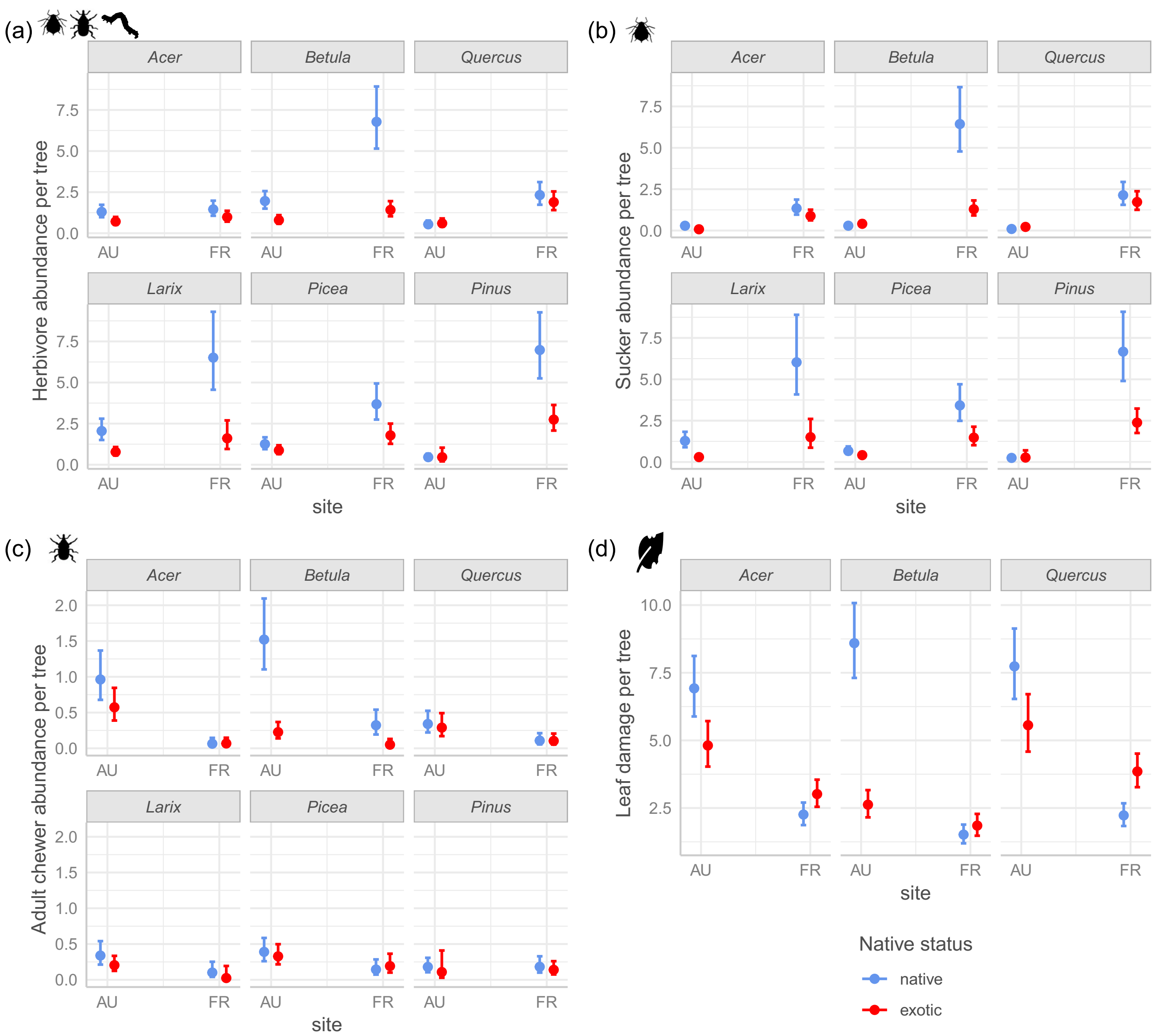

FIGURE 1 Tree-origin effect (native vs. exotic) on insect herbivores in an experiment crossing the biogeographic and community approach for six tree genera. In this figure, a species pair can be compared within a site (AU, North American site; FR, European site), or a species can be compared between continents with inverted native/exotic status. It shows marginal effect plots of (a) total herbivore abundance, (b) sap-sucker abundance, (c) adult leaf-chewer abundance and (d) total leaf damage (not shown for conifers because needle shoots were very rarely damaged). Error bars depict 95% CIs. Mixed effects model structure as described for H1 (multiple fixed effects interactions).

(positive slope estimate of damage ~ abundance, $p < 0.001$; Table 1), but not for Freiburg (negative slope estimate of damage ~ abundance, $p = 0.012$ for interaction between site and abundance; Table 1) in the mixed model set up for assessing this correlation ($N = 892$ trees in 199 plots).

Overall, results for herbivore abundance were consistent with the hypothesis of an inverted within-genus difference among sites corresponding to native versus exotic status (Figure 2). However, not all of the 12 native-exotic comparisons would be significant if tested individually, all estimates (except for one that was close to zero) were negative, indicating a reduced herbivore abundance on the exotic species compared with its native congener. Relatedness among the congeners did not significantly influence the size of the exotic status effect ($p = 0.24$ for interaction between native/exotic status and square-root-transformed intrageneric phylogenetic distance; Table 1; Figure 2; mixed model with random effect of plot, $N = 2054$ trees, 363 plots).

TABLE 1 ANOVA (type III) summary for H1 mixed models evaluating enemy release effects on herbivore abundance and leaf damage.

	Herbivore abundance			Sap-sucker abundance			Adult-chewer abundance			Leaf damage			
Predictor	**df**	χ^2	***p***	**df**	χ^2	***p***	**df**	χ^2	***p***	**df**	**den.df**	***F***	***p***
(Intercept)	1	3.21	0.073	1	32.04	**<0.001**	1	0.05	0.831				
Site	1	0.27	0.603	1	30.62	**<0.001**	1	36.04	**<0.001**	1	160.5	247.16	**<0.001**
Genus	5	77.13	**<0.001**	5	75.69	**<0.001**	5	78.35	**<0.001**	2	453.0	21.46	**<0.001**
Status	1	7.84	**0.005**	1	9.80	**0.002**	1	4.26	**0.039**	1	353.3	11.39	**<0.001**
Site × genus	5	69.81	**<0.001**	5	50.77	**<0.001**	5	21.77	**0.001**	2	453.0	1.57	0.210
Site × status	1	0.44	0.505	1	3.41	0.065	1	0.84	0.361	1	353.3	88.34	**<0.001**
Genus × status	5	15.62	**0.008**	5	32.91	**<0.001**	5	24.72	**<0.001**	2	484.3	13.71	**<0.001**
Site × genus × status	5	6.04	0.302	5	27.37	**<0.001**	5	1.48	0.916	2	484.3	4.78	**0.009**

Note: *p*-values <0.05 are indicated in boldface. den.df are not well defined for the abundance models (generalized linear mixed model), but the no. observations provides comparable information: 2054 trees, 363 plots; for damage models (linear mixed model): 898 trees, 199 plots. Note that we show these type III ANOVA tables for orientation, but they are difficult to interpret given the many interaction terms.
Abbreviation: Status, species origin status at the site, that is native or exotic.

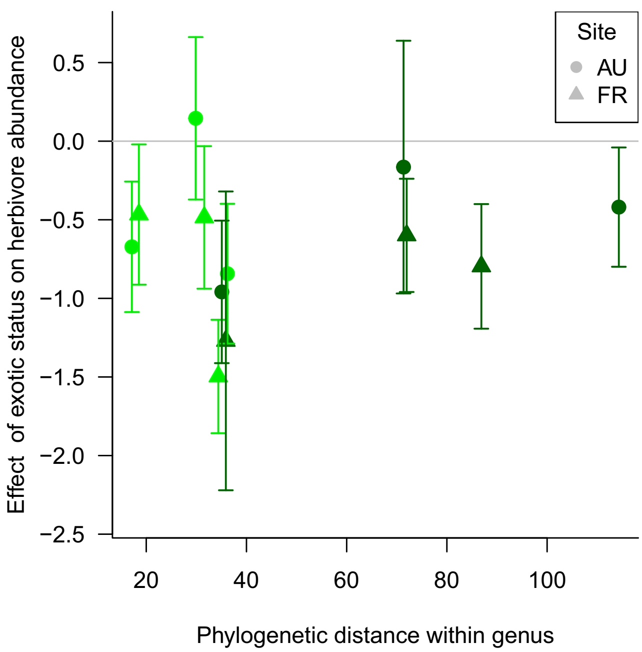

FIGURE 2 Tree-origin effect in relation to intrageneric phylogenetic distance. The *y*-axis shows the estimate for the exotic status effect (difference in herbivore abundance between native species and exotic congener, on a log scale, with 95% CIs) for each genus (i.e., species pair) on each site. Negative estimates are consistent with enemy release. These estimates are equivalent to log-response-ratios, with a value of −1 indicating an almost two-thirds reduction of herbivore abundance on the exotic species compared with its native congener. The *x*-axis shows how closely related the two species being compared are (unit is Ma). Conifers in dark green, broadleaves in light green. The *x*-axis has been slightly jittered to make overlaying lines visible.

H2 Does the effect of exotic status depend on community context (tree diversity)?

The mixed model designed for H2 (random effect of species) confirmed that exotic species generally had lower herbivore abundance (roughly half as much) than native congeners on both sites ($p = 0.001$; see Table 2 for test statistic and additional details for this and other results reported below; Figure 3a). The interaction between tree status and tree diversity (tree species richness in the plot, log transformed) was close to significant ($p = 0.050$; Table 2), thus indicating some trend for stronger effects of exotic status in monocultures than in six-species-mixtures. This also corresponds to a weak trend for herbivore abundance to decrease with tree diversity on native trees, but increase with tree diversity on exotic trees. Nevertheless, herbivore abundance was higher on natives than exotics also in mixture plots.

Results for sap suckers and adult chewers considered separately looked broadly similar (Figure 3b,c). Guild-specific abundance was higher on natives compared with exotics ($p < 0.001$ and $p = 0.001$, respectively; Table 2), and the effect of tree diversity was small, uncertain, and not significant. The interaction between status and tree diversity was not significant ($p > 0.1$; Table 2), with a nonsignificant trend for the status effect to be strongest in monocultures. In difference to all herbivores or sap suckers, the tree-diversity effect on adult-chewer abundance was estimated to be positive (but not significant) for both native and exotic trees.

Leaf damage (on broadleaves) showed the most variable results (Figure 3d) in the H2 model structure. Effects

TABLE 2 Model summaries (parameter estimates and tests) for H2 mixed models evaluating the interaction between enemy release effects and tree-diversity effects.

	Herbivore abundance				Sap-sucker abundance				Adult-chewer abundance				Leaf damage				
Predictor	**Est.**	**SE**	***z***	***p***	**Est.**	**SE**	***z***	***p***	**Est.**	**SE**	***z***	***p***	**Est.**	**SE**	**df**	***t***	***p***
(Intercept)	0.37	0.21	1.73	0.083	−0.76	0.25	−3.09	**0.002**	−0.81	0.17	−4.67	**<0.001**	2.28	0.08	7.99	26.82	**<0.001**
Site FR	0.85	0.17	4.89	**<0.001**	1.94	0.19	9.97	**<0.001**	−1.24	0.14	−8.84	**<0.001**	−1.18	0.11	6.48	−10.37	**<0.001**
Status exotic	−0.81	0.24	−3.43	**0.001**	−0.77	0.23	−3.39	**0.001**	−0.73	0.20	−3.61	**<0.001**	−0.54	0.19	6.01	−2.86	**0.028**
log(SR)	−0.09	0.10	−0.89	0.373	−0.10	0.11	−0.86	0.389	0.17	0.15	1.17	0.240	−0.15	0.06	188.77	−2.60	**0.010**
Status exotic × log(SR)	0.24	0.13	1.96	0.050	0.23	0.15	1.54	0.124	0.30	0.21	1.43	0.152	0.01	0.07	304.50	0.21	0.837
Site FR × status exotic	...	...	...	...	...	...	...	...	...	...	...	...	0.78	0.29	4.01	2.68	0.055
Site FR × log(SR)	...	...	...	...	...	...	...	...	...	...	...	...	0.15	0.07	173.00	2.07	**0.040**

Note: Sap suckers and adult chewers are the largest subset guilds of herbivores. *p*-values <0.05 are indicated in boldface.
Abbreviations: Est., parameter estimate (log scale); FR, site Freiburg; SE, standard error of estimate; SR, tree species richness; Status, species origin status at the site, that is native or exotic.

differed between sites for both, exotic status (with high uncertainty; site by status interaction, $p = 0.055$; Table 2) and tree diversity (significant site by tree-diversity interaction, $p = 0.040$; Table 2). In Auclair, leaf damage was lower (almost halved) on exotics than natives ($p = 0.028$; Table 2) and decreased with tree diversity by one-quarter from monocultures to six-species plots ($p = 0.010$; Table 2). In Freiburg, in contrast, leaf damage was slightly (approximately one-third, with high uncertainty) higher on exotics than natives, whereas leaf damage did not change with tree diversity (less than 5% estimated change from monocultures to six-species mixtures). In any case, there was no indication that the effect of exotic status on leaf damage was contingent on tree diversity (status by diversity effect, $p = 0.837$; Table 2).

DISCUSSION

Here, we have presented the first experimental test of enemy release in a fully crossed cross-continental comparison paired with a community diversity gradient. Our results for herbivore abundance indicate enemy release independent of tree species identity, continent or neighbor tree diversity: more insect herbivores were found on native trees than on their exotic congeners. In contrast, the effect of exotic status on leaf damage was site dependent, with more damage on exotics only in the site with high leaf-chewer abundance. Exotics had lower herbivory (abundance and damage) irrespective of the community context, despite a nonsignificant trend for weaker enemy release in species-rich communities.

Exotic status reduces herbivore abundance, but has variable effects on leaf damage

The higher herbivore abundance on native compared with exotic trees is in agreement with our hypothesis that exotic trees benefit from enemy release. This was found despite reasons for not expecting such an effect in our experimental design. First, enemy release reported in previous studies might be confounded with effects of site or species identity, which we excluded with our fully crossed design comparing pairs of congeners in their native and introduced ranges, thus raising the strength of evidence for exotic status being the cause of low herbivore load. Second, enemy release effects were expected to be weak or absent for generalist herbivores (Bertheau et al., 2010; Morrison & Hay, 2011; Parker et al., 2012), but we found an effect of native versus exotic status for both herbivore guilds, sap suckers (presumably specialized) and adult leaf chewers (presumably generalized). Third, strong enemy release was expected if potential native and exotic hosts are only distantly related to each other (Goßner et al., 2009; Pearse & Hipp, 2014), but here we found enemy release effects among congeneric pairs of native and exotic species, that is pairs of closely related taxa. Based on phylogenetic conservatism (Brändle et al., 2008),

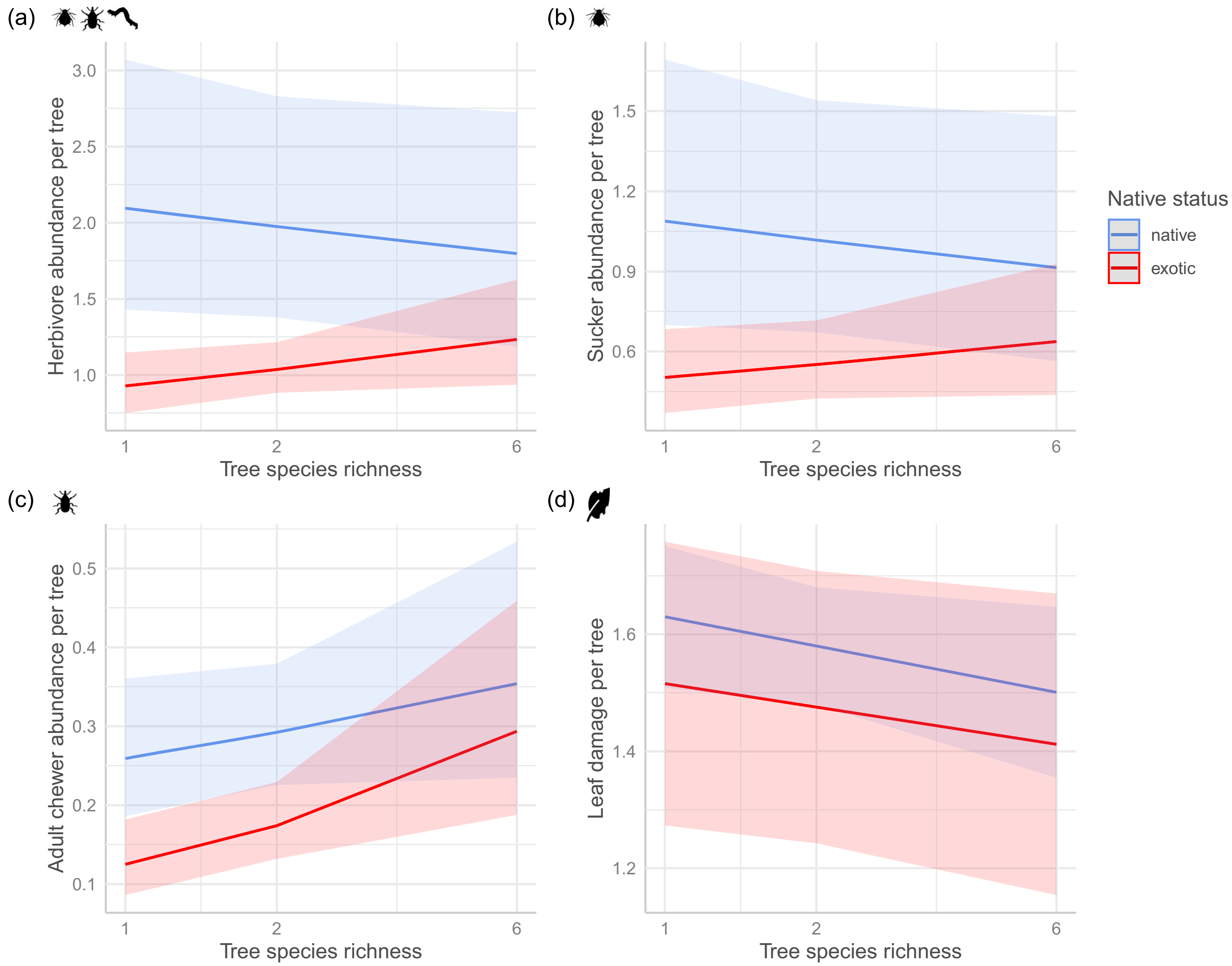

FIGURE 3 Interaction between tree-origin effects and community context (varying tree diversity per study plot). The figure shows marginal effect plots of (a) total herbivore abundance (b) sap-sucker abundance (c) leaf-chewer abundance (d) total leaf damage. Note that (d) only includes damage on broadleaved tree species and excludes conifers (as these had too little damage to be analyzed). Error bars depict 95% CIs. Mixed effects model structure as described for H2 (multiple random effects, which contributed to the large CIs).

enemy release might even be stronger in comparisons among more distantly related taxa than in our comparisons among congeners. However, in our study, the phylogenetic distance between paired native and exotic tree species was not significantly related to the strength of enemy release, which questions the importance of phylogenetic conservatism for insect–herbivore colonization on exotic plants. In any case, our study showed that enemy release did not only apply under specific premises but could be generally expected for exotic trees.

In contrast with effects on herbivore abundance, effects on leaf damage differed between sites. These two herbivory measures had different qualities as indicators of herbivore effects on plant fitness. Leaf damage might be a more direct way of measuring the actual harm to plants (Zvereva et al., 2012), whereas herbivore abundance indicates where herbivores were present at the time of sampling and at what density. Yet, in our study, herbivore abundance represented a larger variety of herbivore guilds and was informative also for conifer trees, whereas leaf damage assessment gave an incomplete picture as it reflected almost only leaf-chewer damage on broadleaved trees. The most commonly sampled chewers (adult weevils) are generalist herbivores (Pinski et al., 2005a), which are expected to respond less consistently to exotic status than specialists. Although attributing observed damage to observed herbivores remains uncertain, a positive correlation between (chewer) leaf damage and chewer abundance at least in Auclair suggests that most of the observed leaf damage was due to the sampled chewers.

In Auclair, both chewer abundance and leaf damage were more pronounced on native than exotic trees. This finding is in line with our first hypothesis. In Freiburg, however, leaf damage was marginally lower on natives than on exotics. As an earlier study at the Freiburg site did not find a difference in leaf damage between native and exotic tree species (Wein et al., 2016), the pattern for our sampling year may have been a special case. A speculative explanation for why, in Freiburg, chewer abundance and leaf damage tended to respond in opposite ways could be a lack of co-evolution of North American trees with local herbivores (Morrison & Hay, 2011). This lack of co-evolution might allow exotic trees to escape the host finding of herbivores, but when those insects are on the tree, native trees may be less able to defend themselves and suffer more damage (see also Agrawal et al., 2005). Unexpectedly, the main leaf-chewing weevils we observed were themselves exotic in North America (Pinski et al., 2005b), which means that the observed lower herbivory on exotics in Auclair is not true enemy release, but rather conforms to the "enemy-of-my-enemy hypothesis" (Colautti et al., 2004; Enders et al., 2020), which states that (introduced) enemies of native plants help the success of exotic plants. From this perspective, leaf damage results make sense across the two sites: the generalist chewing weevils native to Europe may feed more strongly on trees native to North America, which gives them a preadaptation to invade North American forests and causes an apparent enemy release effect in the North American IDENT site (Belluau et al., 2021). A preference for exotic plant species (when encountered) is consistent with preliminary feeding choice experiments we performed in Freiburg (unpublished data) and has been shown for other generalist herbivores (Morrison & Hay, 2011; Parker et al., 2006). Overall, a more complex mechanism for generalist chewer abundance and damage combined with enemy release from specialist sap suckers leads to consistently lower herbivory for exotic trees on both continents and on average across the six tree genera.

Enemy release in a community context

We predicted that enemy release effects become weaker with increasing tree diversity. However, reduced herbivory on exotic tree species appeared to be mostly independent of plot tree diversity. The difference between native and exotic trees decreased marginally with increasing tree diversity, was characterized by high uncertainty, and was only observed for total herbivore abundance (not for leaf damage). We had expected that specialized herbivores would not find native host trees in mixtures as easily if masked by neighboring trees and that herbivores from native trees could spill over onto exotic trees in mixtures, but there was limited evidence for such an influence of community diversity for either herbivore guild. Reduced herbivory on exotics was also observed in mixed-species plots, which added to our rejection of specialization and phylogenetic isolation expectations in making reduced herbivory a general phenomenon for exotic trees.

Despite the expectation of AR for sap-sucking insects (as a mostly specialized herbivore guild), no significant tree-diversity effect on the abundance of either herbivore guild was found. Nevertheless, there was a minor trend that diversity reduced abundance only of the more specialized herbivore guild and only on native trees, whereas abundance tended to increase for the more generalized herbivore guild on natives and for both guilds on exotics. Our expectations regarding diversity effects cannot be completely rejected, but possible diversity effects were small compared with effects of exotic status. For leaf damage, the effect of tree diversity tended to depend on the site. At the Freiburg site, a trend toward increasing damage with increasing tree diversity confirmed an earlier study conducted at the same site (Wein et al., 2016), and was consistent with the expectation of ASs for generalist herbivores (Barbosa et al., 2009; Schuldt et al., 2015). In contrast, our finding of declining damage with increasing tree diversity in Auclair was more surprising. This observation suggested that tree diversity provides biotic resistance against invasive weevils in Canada (consistent with the biotic resistance hypothesis sensu Enders et al., 2020), where these generalist exotic herbivores have apparently acquired abilities to find new hosts in monocultures.

Tree-diversity effects, including their influence on enemy release, should be interpreted with caution regarding the transferability to real-world forests, as the plots in the experiment were small and diversity effects at a small scale may also be influenced by the surroundings. Conversely, the enemy release observed at the small scale might be even stronger in larger plots as they allow arthropod population dynamics to build up over time. Obviously, extrapolations for very long time scales should be made with caution, as native herbivores might increasingly adapt to the novel feeding options provided by exotic species (Brändle et al., 2008; Strong et al., 1984) or more specialized original enemies might arrive at the exotic sites.

Conclusions

Our study detected significantly lowered herbivory for exotic tree species in a cross-Atlantic study. Use of a full-factorial, systematic comparison of native and exotic tree species made it possible to tease apart the effects of native versus exotic tree origin from the effects of tree species identity, study site, and community context. We showed that reduced herbivory on exotic trees was independent of tree species identity and of the diversity of the surrounding tree community. Also, reduced herbivory did not depend on the exotic tree being highly invasive or phylogenetically distant from native species. Lower herbivore loads could thus be expected generally for exotic tree species. Nevertheless, continued efforts are needed to understand the behavior and adaptation of herbivorous insects (including insects that are exotic themselves) faced with novel tree communities and the resulting impacts on trees. If we need to use nonnative tree species to adapt our forests to climate change, then even congeneric species of those that may be replaced or complemented will probably experience less herbivory, at least for some time.

AUTHOR CONTRIBUTIONS

Sylvie Berthelot and Jochen Fründ designed the study. Christian Messier, Alain Paquette, and Peter B. Reich designed the overall network of diversity experiments (IDENT). Jürgen Bauhus designed and established IDENT-Freiburg jointly with others. Charles A. Nock established and maintained IDENT-Freiburg. Dominique Gravel designed and established IDENT-Auclair jointly with others. Sylvie Berthelot collected the data. Sylvie Berthelot and Jochen Fründ performed the analysis and prepared the manuscript with contributions from all authors. Jochen Fründ provided guidance throughout the study and prepared the revision. All authors read, reviewed, and approved the final version of the paper.

ACKNOWLEDGMENTS

We thank Michael Scherer-Lorenzen and Simon Bilodeau-Gauthier, who established and maintained the IDENT-Freiburg experiment together with Jürgen Bauhus and Charles A. Nock. We thank Jonathan Brassard, Justine Fontaine-Topaloff, and Leon Thoma, who helped with data collection in IDENT-Auclair and Deena Shrestha, who helped with data collection in IDENT-Freiburg. The establishment and maintenance of IDENT-Freiburg and IDENT-Auclair would not have been possible without the help of numerous students, technicians, and volunteers. This work was supported by a grant from the Baden-Württemberg Stiftung (Elite program for postdocs, 1.16101.17) to Jochen Fründ. We also thank the United States National Science Foundation Biological Integration Institutes grant no. NSF-DBI-2021898 and an NSERC discovery grant to Christian Messier for support. We thank two anonymous reviewers for their helpful comments. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and analysis code (Berthelot et al., 2023) are available in Dryad at https://doi.org/10.5061/dryad.1zcrjdfxd.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Berthelot, Sylvie, Jürgen Bauhus, Carsten F. Dormann, Dominique Gravel, Christian Messier, Charles A. Nock, Alain Paquette, Peter B. Reich, and Jochen Fründ. 2023. "Exotic Tree Species Have Consistently Lower Herbivore Load in a Cross-Atlantic Tree Biodiversity Experiment." *Ecology* 104(7): e4070. https://doi.org/10.1002/ecy.4070