

Enemy damage of exotic plant species is similar to that of natives and increases with productivity

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Summary

1. In their colonized ranges, exotic plants may be released from some of the herbivores or pathogens of their home ranges but these can be replaced by novel enemies. It is of basic and practical interest to understand which characteristics of invaded communities control accumulation of the new pests. Key questions are whether enemy load on exotic species is smaller than on native competitors as suggested by the enemy release hypothesis (ERH) and whether this difference is most pronounced in resource-rich habitats as predicted by the resource–enemy release hypothesis (R-ERH).

2. In 72 populations of 12 exotic invasive species, we scored all visible above-ground damage morphotypes caused by herbivores and fungal pathogens. In addition, we quantified levels of leaf herbivory and fruit damage. We then assessed whether variation in damage diversity and levels was explained by habitat fertility, by relatedness between exotic species and the native community or rather by native species diversity.

3. In a second part of the study, we also tested the ERH and the R-ERH by comparing damage of plants in 28 pairs of co-occurring native and exotic populations, representing nine congeneric pairs of native and exotic species.

4. In the first part of the study, diversity of damage morphotypes and damage levels of exotic populations were greater in resource-rich habitats. Co-occurrence of closely related, native species in the community significantly increased the probability of fruit damage. Herbivory on exotics was less likely in communities with high phylogenetic diversity.

5. In the second part of the study, exotic and native congeneric populations incurred similar damage diversity and levels, irrespective of whether they co-occurred in nutrient-poor or nutrient-rich habitats.

6. *Synthesis.* We identified habitat productivity as a major community factor affecting accumulation of enemy damage by exotic populations. Similar damage levels in exotic and native congeneric populations, even in species pairs from fertile habitats, suggest that the enemy release hypothesis or the R-ERH cannot always explain the invasiveness of introduced species.

Key-words: biotic resistance, Central Europe, enemy release hypothesis, herbivores, host shifting, invasion ecology, plant invasions, resource availability

Introduction

Exotic plants are likely to lose some of the enemies from their home ranges during the colonization of new continents (Colautti *et al.* 2004; Liu & Stiling 2006). Decreased enemy richness or damage may translate into increased demographic performance (DeWalt, Denslow & Ickes 2004; Roy *et al.* 2011) and thus promote the spread of exotic species and

increase their impact on native communities (Mitchell & Power 2003; but see van Kleunen & Fischer 2009). Loss of herbivores and pathogens, however, is very often compensated for by new interactions with enemies in the colonized range (Mitchell *et al.* 2006). Exotic plants can be used as a food source by insect herbivores (Agrawal *et al.* 2005; Dawson, Burslem & Hulme 2009; Hill & Kotanen 2009) or can be subjected to attack by fungal pathogens (Blaney & Kotanen 2001; Agrawal *et al.* 2005; Parker & Gilbert 2007; Dostál 2010). As the new interactions can limit the success of

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newcomers in colonized communities (Maron & Vilà 2001; Levine, Adler & Yelenik 2004), it is of basic and practical importance to identify which factors determine accumulation of enemies in new ranges.

Exotic species with a longer residence time in their new range or those that have colonized a larger area probably have more natural enemies (Lawton & Strong 1981; Hawkes 2007; Mitchell *et al.* 2010). However, enemy accumulation over time can be slow (Mitchell *et al.* 2010), and time since introduction, or invaded area, may be poorly related to local interactions with herbivores and pathogens (Torchin & Mitchell 2004; Carpenter & Cappuccino 2005). Instead, enemy load for exotic species, and potentially also their invasiveness, may be better explained by the type of communities that they have invaded. Several community characteristics might be important: in particular resource availability, the relatedness between native species and exotic colonizers and native species diversity are expected to have large effects on the degree of herbivory or pathogen attack suffered by exotic species (Agrawal, Lau & Hambäck 2006).

Exotic species are expected to suffer greater enemy attack in fertile environments. As predicted by the growth rate hypothesis (Coley, Bryant & Chapin 1985), species from productive habitats grow fast but are poorly defended, whereas species of infertile sites are less able to replace lost tissue and thus should invest more in constitutive herbivore defence. Although a recent multispecies study did not find a consistent relationship between growth rate and constitutive defence (Kempel *et al.* 2011), meta analyses by Cebrian & Duarte (1994) and by Endara & Coley (2011) supported the growth rate hypothesis by showing that fast growing species suffer higher herbivory rates than slow growing species do. Increased susceptibility to enemies in fertile sites can also be due to high tissue nutrient concentrations (Mattson 1980; Reich, Walters & Ellsworth 1997).

The phylogenetic structure of the community may also play a role if the presence of closely related native plants allows host shifts of oligophagous herbivores and pathogens onto exotic species (Darwin's naturalization hypothesis) (Gilbert & Webb 2007; Dawson, Burslem & Hulme 2009; Hill & Kotanen 2009; Ness, Rollinson & Whitney 2011). Exotic species are also expected to be exposed to more herbivory in less diverse communities, either because of a reduced efficiency of predators (or parasitoids) of herbivorous insects or because of a higher density of specialized insect herbivores (Elton 1958; Root 1973). However, the opposite is also possible if generalist herbivores are more common in species rich communities (Siemann *et al.* 1998; Scherber *et al.* 2010). All three community characteristics mentioned – habitat fertility, relatedness to the native community and native species diversity – can influence the accumulation of enemies and thus potentially their impact on exotic species. However, these factors have usually been studied in isolation (e.g. habitat moisture in a study by Blaney & Kotanen 2001 and relatedness in a study by Ness, Rollinson & Whitney 2011), and their relative importance in influencing enemy accumulation on exotic species remains unclear.

Although exotic species may accumulate some enemies in their introduced ranges, they are still expected to harbour fewer enemies than native species (Torchin & Mitchell 2004), which potentially provides a competitive advantage to the exotics [the enemy release hypothesis (ERH); Keane & Crawley 2002]. Curiously, comparisons between exotic and resident native species in enemy load have yielded mixed results (reviewed by Colautti *et al.* 2004; Liu & Stiling 2006; Chun, van Kleunen & Dawson 2010). It has therefore been suggested that only some exotic species accumulate fewer enemies and that this depends on the resource availability of the environment. According to the resource enemy release hypothesis (R ERH; Blumenthal 2005, 2006), species of more fertile habitats should support more herbivores and pathogens in their home ranges and also lose more of these enemies without replacement in novel ranges. This assumption stems from the growth rate hypothesis (Coley, Bryant & Chapin 1985), which predicts that species of resource rich habitats are particularly susceptible to enemies and therefore should benefit most from a paucity of enemies in their new range. Blumenthal *et al.* (2009) found support for habitat fertility driven pathogen diversity in the native range, as well as loss in the novel range. What remains untested, however, is whether the difference in enemy diversity and damage between exotic and native species is larger in fertile than in nutrient poor habitats, as also predicted by the R ERH.

In the first part of our study, we assessed the relative influence of the three different groups of community predictors (habitat fertility, relatedness between exotic species and the native community and native species diversity) on damage diversity and levels for the exotic species. We scored all above ground, visible, damage morphotypes caused by herbivores, along with the presence of fungal pathogens, in 72 populations of 12 exotic species invasive to Central Europe. We also estimated levels of leaf herbivory and fruit damage. Community predictors were derived from measurements of standing biomass and native species composition and diversity.

In the second part of this study, we carried out a community comparison (*sensu* Colautti *et al.* 2004) between exotic and native species in damage type diversity and damage levels. We used 28 pairs of co occurring native and exotic populations, representing nine congeneric pairs of native and exotic species. We expected that damage would be larger on native than on exotic species, as the ERH hypothesis predicts (Keane & Crawley 2002), and that the difference would increase with habitat fertility, as the R ERH hypothesis predicts (Blumenthal 2005, 2006).

Materials and methods

SPECIES AND SITE SELECTION

In the first part of this study, where we tested the effect of three different groups of predictors on variation in damage diversity and levels, we included 12 exotic species represented by 72 populations in total (at least five populations per exotic species; Appendix S1,

Table 1). All 12 species are naturalized in the Czech Republic, and 10 of them are considered invasive (Pyšek, Sádlo & Mandák 2002). In the second part of this study, where we tested the ERH and R ERH hypotheses, we included nine exotic species and eight native congeneric species [Table 1; exotic species *Conyza canadensis* (also *Erigeron canadense*) and *Erigeron annuus* shared the same native congener *Erigeron acer*]. Exotic species were represented by 28 populations that were also included in the first part of the study, but here we used only those that co occurred with populations of native congeners (Appendix S1, Table 1).

All study populations contained at least 100 individuals per species and were located in central and north west Bohemia (the Czech Republic). More details on site survey and species selection are provided in Dostál (2011). Some sites had populations of more than one exotic species or of more than one congeneric pair (Appendix S1).

MEASUREMENT OF HABITAT FERTILITY AND OTHER COMMUNITY PARAMETERS

Three groups of community predictors were measured: (i) habitat fertility, (ii) relatedness of exotics to native species in the communities and (iii) species diversity. As a proxy for habitat fertility, we measured habitat productivity, which has been shown to be linked to soil resource availability (e.g. Baer *et al.* 2003). We did so by sampling herbaceous standing biomass between July and August 2008, during peak productivity of the vegetation. At each site, we harvested native species biomass 2 cm above the ground in five randomly selected 25 × 25 cm squares. Biomass was then dried to constant mass at 70 °C. Fertility was also estimated using mean Ellenberg indicator values for moisture and nutrients, of native species (Ellenberg *et al.* 1992). The system of Ellenberg indicator values for several environmental characteristics has been developed for c. 3000 vascular plant species occurring in the western part of Central Europe, and indicator values for nutrients are supposed to reflect the availability of nitrogen (Ellenberg *et al.* 1992). Diekmann (2003), in his review, documented that mean indicator value for nutrients calculated from species present at a site can be poorly related to the total amount of nitrogen or total nitrogen mineralization rate at the site. However, the

mean indicator value nevertheless reflects well the amount of ammonium or nitrate ions and other macronutrients (P, K) in the soil. It is also correlated with the standing crop and nitrogen accumulation in plants (Diekmann 2003). In our previous study (Dostál *et al.* 2013), we found that the maximum growth rate of 74 Central European species was positively correlated with mean indicator value for nutrients of their habitat calculated from co occurring species. In line with the growth rate hypothesis posited by Coley, Bryant & Chapin (1985), it can be expected that species from habitats with higher indicator values for nutrients will experience more herbivory.

The composition and abundance of native species were determined in three plots of 2 × 2 m at each site during the same period as biomass sampling. Plots were located at a minimum distance of 10 m from each other and exotic species cover in the plots had to be < 10%, to reflect likely conditions prior to invasion. Relatedness was expressed as phylogenetic distance to the nearest native neighbour in the community, mean phylogenetic distance to all native species in the community and phylogenetic distance to the dominant species in the community. The calculation of phylogenetic distances is described in Appendix S2. We used two measures of native plant diversity: first, the cumulative number of native species (species richness) present in three plots per site and secondly, the phylogenetic diversity of the native community, calculated as the mean pairwise phylogenetic distance between all pairs of native species (MPD) (Appendix S2).

Sampling only three plots may underestimate species richness present at the study sites. To test this, we used vegetation data collected in 2008 (i.e. three plots/site) and calculated asymptotic minimum species richness and the additional sampling effort needed to reach the asymptotic richness, according to algorithms described by Chao *et al.* (2009). We found that asymptotic minimum species richness was indeed larger than observed species richness but the two were positively correlated. More importantly, the additional sampling effort needed to reach asymptotic richness was independent of the observed richness. Therefore, our approach underestimates species richness, but similarly across differently diverse communities (Appendix S3).

Sampling only three plots may also be insufficient to detect the nearest native neighbour in the community. To explore this, we went

Species	Habitat productivity (g m ⁻²) (mean ± SD)
Asteraceae	
E: <i>Bidens frondosa</i> ₁₉₀₀ N: <i>Bidens radiata</i>	655.4 ± 45.8 (n = 2 sites)
E: <i>Conyza canadensis</i> ₁₇₈₉ N: <i>Erigeron acer</i>	391.9 ± 75.5 (n = 2 sites)
E: <i>Erigeron annuus</i> ₁₈₈₄ N: <i>Erigeron acer</i>	356.1 ± 75.5 (n = 2 sites)
E: <i>Matricaria discoidea</i> ₁₈₅₁ N: <i>Matricaria chamomilla</i>	122.6 ± 19.1 (n = 4 sites)
E: <i>Solidago canadensis</i> ₁₈₃₈	400.2 ± 73.7 (n = 5 sites)
Balsaminaceae	
E: <i>Impatiens parviflora</i> ₁₈₇₀ N: <i>Impatiens noli tangere</i>	231.4 ± 109.4 (n = 4 sites)
Brassicaceae	
E: <i>Bunias orientalis</i> ₁₈₅₆	765.9 ± 196.9 (n = 6 sites)
Crassulaceae	
E: <i>Sedum hispanicum</i> ₁₉₅₄ N: <i>Sedum acre</i>	153.9 ± 24.5 (n = 3 sites)
Juncaceae	
E: <i>Juncus tenuis</i> ₁₈₅₁ N: <i>Juncus effusus</i>	178.5 ± 62.9 (n = 3 sites)
Leguminosae	
E: <i>Trifolium hybridum</i> ₁₈₀₉ N: <i>Trifolium repens</i>	238.6 ± 71.7 (n = 5 sites)
E: <i>Lupinus polyphyllus</i> ₁₈₉₅	237.9 ± 107.0 (n = 6 sites)
Onagraceae	
E: <i>Epilobium ciliatum</i> ₁₉₆₀ N: <i>Epilobium hirsutum</i>	443.6 ± 148.1 (n = 4 sites)

Table 1 Exotic (E) and native (N) congeners used in this study, with information on plant family and year of introduction of exotic species to Central Europe according to Pyšek, Sádlo & Mandák (2002). Mean habitat productivity is provided for sites included in the ERH/R ERH test. Habitat productivity is also shown for the three exotic species (*Bunias orientalis*, *Lupinus polyphyllus* and *Solidago canadensis*) that were only included in the first part of this study

back to 10 study sites in late June 2012 and recorded native species in six plots per site. We then randomly sampled from one to five plots (of six) and identified the phylogenetic distance to the closest native species present in the sample. Although the distance to the closest native relative tended to decrease when more plots were sampled, this decrease was not statistically significant, meaning that increased sampling would not have significantly altered our measure of mean nearest neighbour distance (Appendix S3).

MEASUREMENT OF DAMAGE DIVERSITY AND DAMAGE LEVELS

Enemy exclusion experiments provide the most accurate assessments of the extent to which plant enemies control the performance of exotic plants and reduce their invasiveness (Blaney & Kotanen 2001; DeWalt, Denslow & Ickes 2004; Dostál 2010; Roy *et al.* 2011). These experiments are, however, time consuming, and use of pesticides or enclosures may have confounding side effects. Thus, studies testing the ERH often use enemy species richness as a proxy instead (Agrawal *et al.* 2005; Mitchell & Power 2003; van Kleunen & Fischer 2009). Many studies testing the ERH or those searching for biotic resistance of invaded communities also frequently use leaf herbivory (Agrawal *et al.* 2005; Carpenter & Cappuccino 2005; Dawson, Burslem & Hulme 2009) or fruit damage (Hill & Kotanen 2011) as a proxy for enemy regulation, and we also use these proxies here. We also applied a method used mainly in palaeoecology that estimates herbivore pressure on plants from the diversity of insect damage types. Wilf & Labandeira (1999) analysed fossilized insect damage types and detected more plant herbivore interactions in the warmer Eocene than in the cooler Palaeocene. In our study, we used the diversity of damage morphotypes to assess the differences in plant herbivore and plant pathogen interactions among invaded plant communities. Damage type diversity has also been used recently in a study testing the ERH (Roy *et al.* 2011) and a study exploring biotic resistance (Harvey *et al.* 2012).

In 2008 and 2009, between July and September, at the onset of the fruiting period of the respective target species, we randomly picked 20 individuals in each population and scored them for all visible above ground damage morphotypes caused by herbivores, as well as for the presence of fungal pathogens.

We distinguished nine groups of damage morphotypes or enemies:

- 1 Powdery mildew: pathogenic fungi belonging to the order Erysiphales, which causes white powdery spots on the leaves and stems of infected plants.
- 2 Rust fungi: pathogenic fungi belonging to the order Uredinales, which causes reddish spots on infected plants.
- 3 Herbivory by mammalian herbivores: in contrast to insect herbivory, attacked plants were missing whole leaves or parts of the stems.
- 4 Phloem feeding aphids.
- 5 Insect leaf herbivory: this was indicated by perforations and missing parts of leaves due to feeding by a wide range of insects.
- 6 Leaf mining: this is caused by larvae that live in and eat the leaf tissue of plants. Leaf miners include many different species of insects but most of them are moths (Lepidoptera) and flies (Diptera).
- 7 Pre dispersal fruit damage: the presence of holes in fruits or seeds or missing fruit parts observed on propagules that were still attached to the mother plant. This damage could be caused by a

wide range of insects. We also observed some species specific symptoms of fruit attack such as the presence of psyllid galls in plants of the genus *Juncus* (genus *Livia*, Psyllidae, Homoptera).

- 8 Stem boring: the most apparent sign of this damage type is the presence of holes or rather a single hole in the lower part of the stem. It is caused by a female insect that chews the hole and deposits one or more eggs in it. After hatching, larva/larvae penetrate to the centre of the stem and burrow into it or into the rhizomes (i.e. below ground stems). Stem borers include taxa from the orders Hymenoptera, Diptera, Coleoptera and Lepidoptera.
- 9 Scraping on the stems: this damage type was most likely caused by molluscs.

In addition, we quantified levels of leaf herbivory and pre dispersal fruit damage for the same individuals as those used in damage type screening. To quantify leaf herbivory, we randomly picked five leaves per plant and assessed the fraction of leaf area removed by herbivores. Missing leaf area was recorded on a four degree scale: (i) no sign of herbivory; (ii) 1 25% missing; (iii) 26 50% missing; (iv) 51 100% missing. For further calculations, each degree scale was substituted by the average of the respective interval, that is, by 0%, 12.5%, 37.5% and 75%, respectively. Level of fruit damage per plant was estimated as the proportion of fruits with symptoms of insect attack, of five randomly selected fruits. For each population, we calculated average damage levels across the 20 screened individuals.

In 2008, 100 populations were scored. In 2009, the number of populations was 96 as two exotic populations and two native populations could not be scored due to small population sizes in that year or due to site destruction. In total, we scored 3920 plant individuals and 19 600 leaves and 19 600 fruits.

STATISTICAL ANALYSES

Community predictors of damage diversity and damage levels on exotics

We searched for minimum adequate models (MAMs) including those community parameters, of eight potential predictors that best explained the variation in damage diversity and damage levels on exotics. We used an approach similar to that used by Mitchell *et al.* (2010), where we did not evaluate all possible combinations of parameters in our models but instead constructed a subset of models based on grouping the predictor variables. We included a full model with all eight factors from three predictor groups: habitat fertility characteristics, relatedness between the exotic and the native community and native species diversity (see Appendix S4). We then compared this to models with all predictors from two of the predictor groups but with only one of the possible combinations of predictors from the third group, including one to $n - 1$ predictors, where n is the number of predictors in the third group. We also constructed models including two predictor groups only, with one kept constant and the other one changed as described for the previous step. Finally, we tested models with only one group of predictors. We also added a model without any of the three predictor groups. All models included year as a fixed term and plant family, species identity and site as random terms. Explanatory variables were standardized to zero mean and unit variance to facilitate comparisons of the estimates (Schielzeth 2010).

For each of six response variables listed below, we therefore ran 67 models (Appendix S4), and we identified the best models on the

basis of Akaike Information Criterion (AIC) and AIC weights. The AIC weights calculate the relative support for each model compared to all other models. Using the AIC weights, we then assembled the 95% confidence sets of models, that is, the set of models whose AIC weights sum to 95%. As a complementary approach, for each predictor, we also summed the AIC weights of all the models that included that variable. As all predictors were present in an equal number of models (Appendix S4), this sum indicates the relative importance of the respective predictor, independent of the other predictor variables. To check for potential problems of collinearity, correlation matrices of explanatory variables were calculated prior to analyses (see Appendix S5). All but one of the correlations were below 0.7 (the rule of thumb level suggested by Gujarati 1995), suggesting that multicollinearity was not a major issue.

Damage diversity and damage levels were expressed by six different response variables: (i) mean damage diversity (mean from 20 individuals per population), (ii) cumulative damage diversity (all damage types detected on the 20 individuals per population), (iii) presence of leaf herbivory, (iv) presence of damaged fruits, (v) mean proportion of leaf herbivory and (vi) mean proportion of damaged fruits. Only populations with mean leaf herbivory and mean proportion of damaged fruits >0% were used to calculate the response variables (v) and (vi), respectively. Both damage diversity measures were $\ln(x + 1)$ transformed to meet assumptions of homoscedasticity and normality of residuals. Mean proportions of leaf herbivory and damaged fruits were arc sine square root transformed.

We also re ran all above models with identical predictor groups but (i) with different relatedness metrics as predictors and (ii) with plant size as a covariable. Regarding the different relatedness metrics, we used inverse pairwise distance between exotic and native species (inverse nearest neighbour distance, inverse distance to native community dominant species and mean of inverse phylogenetic distance to all native species in the community) after Ness, Rollinson & Whitney (2011). These inverse metrics assume a nonlinear increase in interaction strength with relatedness, with closely related species being weighted more heavily than distantly related ones (Ness, Rollinson & Whitney 2011).

Plant size represented by canopy height (obtained from the LEDA trait data base; Kleyer *et al.* 2008) of a species was used as a covariable because larger organisms may have more enemy individuals or species (Poulin & Morand 2004; Mitchell *et al.* 2010). At the same time, species with greater canopy height tended to occur in more fertile habitats (see Appendix S6). So, we were interested how the effect of habitat fertility on damage diversity and damage levels changes after differences in canopy height of species were controlled for.

ERH/R-ERH test

The R ERH predicts that the difference between native and exotic species in enemy load should increase along a productivity gradient. For the ERH/R ERH test, we thus included the nine congeneric pairs of exotic and native species occurring in habitats that differed considerably in productivity, as expressed by standing biomass. Whereas some grew in resource poor sites, such as road verges or scree slopes, with mean habitat productivities of 123 g m^{-2} or 154 g m^{-2} (the *Matricaria* pair and the *Sedum* pair, respectively), the *Bidens* congeneric pair was confined to very fertile sites: fish pond banks with a productivity of 655 g m^{-2} (Table 1).

We used linear mixed models to test for the fixed effects of habitat productivity, species origin (native vs. exotic) and their interaction,

along with year of sampling (2008 and 2009), on damage diversity and damage levels. Plant family, species identity and site were used as random terms. Plant family was included to correct, at least to some extent, for possible phylogenetic signal in damage diversity and levels (e.g. Hill & Kotanen 2011). Six separate models were run, each one with a different response variable as defined in the first part of the study. Addition of a quadratic term for habitat productivity did not improve the fit of any model (not shown), so we report models with a linear term for natural log transformed productivity only. Statistical significance of fixed effects was estimated by comparison of models using log likelihood ratio tests. We also evaluated two additional models with the difference between the native and exotic species, in mean and cumulative damage diversity, as response variables and productivity and year as fixed effect predictors.

There are three possible confounding factors that could influence the ERH/R ERH test. First, differences in damage need not reflect a different plant origin but could be rather a consequence of trait dissimilarity of the compared groups (Agrawal *et al.* 2005; Blumenthal 2006). Second, evidence in favour of the R ERH could be masked if species from fertile habitats also have a longer invasion history in the new range and thus have accumulated more enemies (e.g. Hawkes 2007). Third, a test of the R ERH could be confounded if phylogenetic distance between species within congeneric pairs is significantly related to habitat productivity. However, we found no significant evidence for any of these three possible confounding factors (see Appendix S6).

In all analyses, we fitted linear mixed models in *lme4* (Bates 2010) of R version 2.11.0 (R Development Core Team 2010). Binomial errors were used in models with presence/absence of leaf herbivory and damaged fruits as response variables.

Results

COMMUNITY PREDICTORS OF DAMAGE DIVERSITY AND DAMAGE LEVELS ON EXOTICS

Damage diversity and damage levels on exotic populations increased with habitat fertility (Table 2a, Fig. 1 and Appendix S7). For five of the six response variables, habitat fertility descriptors were always present in at least one of the three best models (based on AIC values) (Table 2a). Based on summed AIC weights (Appendix S7), standing biomass was the most important variable that positively influenced mean damage diversity and mean proportion of leaf herbivory (Table 2a and Fig. 1a,b). Ellenberg indicator values for nutrients and moisture were the best predictors of cumulative damage diversity and mean proportion of damaged fruits, respectively (Table 2a and Fig. 1c,d).

The other two predictor groups relatedness and community diversity were less important but they influenced the presence of damaged fruits and herbivory (Table 2a). Specifically, the presence of closely related native species in the community significantly increased the probability of fruit attack (Fig. 2a). Herbivory was less likely in communities with a high phylogenetic diversity (Fig. 2b). However, phylogenetic diversity was an important predictor (in terms of AIC weight) only when inverse relatedness metrics were fitted in the models (Table 2b and Appendix S7). Fitting inverse relatedness metrics also changed the model selection and related

Table 2 (a) The model selection for each of the six response variables, describing damage diversity and damage levels. The three models with the highest AIC weights are presented (see Appendix S7 for all the models in the 95% confidence set). EIV moisture and EIV nutrients are environmental characteristics of the habitats, estimated from indicator values of co occurring native species after Ellenberg (Ellenberg *et al.* 1992); PhND, phylogenetic distance to the nearest native neighbour; PhMD, mean phylogenetic distance to all native species in the community; PhDD, phylogenetic distance to the dominant native species; MPD, phylogenetic diversity calculated as the mean pairwise phylogenetic distance among all pairs of native species in the community. All models also included year of sampling (2008 or 2009). (b) The model selection with relatedness predictors expressed as inverse relatedness measures

Habitat fertility characteristics (Standing biomass, EIV moisture, EIV nutrients)	Relatedness (PhND, PhMD, PhDD)	Diversity (Richness, MPD)	AIC	Log likelihood	AIC weight
(a)					
Mean damage diversity					
Standing biomass			-24.5	19.2	0.24
Standing biomass, EIV moisture			-23.0	19.5	0.11
Standing biomass, EIV nutrients			-22.6	19.3	0.10
Cumulative damage diversity					
EIV nutrients			46.0	-16.0	0.19
Standing biomass, EIV nutrients			47.3	-15.6	0.10
EIV moisture, EIV nutrients			47.9	-15.3	0.08
Mean proportion of leaf herbivory					
Standing biomass, EIV nutrients			-249.9	132.9	0.19
Standing biomass			-249.8	131.9	0.17
Standing biomass, EIV moisture, EIV nutrients			-248.2	133.1	0.08
Mean proportion of damaged fruits					
EIV moisture, EIV nutrients			-131.8	73.9	0.14
Standing biomass, EIV moisture, EIV nutrients	PhDD		-130.8	75.4	0.08
EIV moisture, EIV nutrients	PhND, PhMD, PhDD		-130.6	76.3	0.07
Presence of leaf herbivory					
		MPD	63.6	-25.8	0.11
Standing biomass, EIV moisture			65.1	-25.5	0.05
			65.4	-27.7	0.04
Presence of damaged fruits					
	PhND		148.7	-68.4	0.21
	PhND, PhDD		149.7	-67.9	0.13
	PhND, PhMD		150.7	-68.3	0.08
(b)					
Mean damage diversity					
Standing biomass			-24.5	19.2	0.15
Standing biomass, EIV moisture			-22.9	19.5	0.07
Standing biomass, EIV moisture, EIV nutrients	iPhND		-22.8	21.4	0.07
Cumulative damage diversity					
EIV nutrients			46.0	-16.0	0.21
Standing biomass, EIV nutrients			47.2	-15.6	0.11
EIV moisture, EIV nutrients			47.9	-15.9	0.08
Mean proportion of leaf herbivory					
Standing biomass, EIV nutrients			-249.9	132.9	0.17
Standing biomass			-249.8	131.9	0.16
Standing biomass, EIV moisture, EIV nutrients			-248.2	133.1	0.07
Mean proportion of damaged fruits					
EIV moisture, EIV nutrients	iPhND, iPhMD, iPhDD	Richness, MPD	-135.9	80.9	0.26
Standing biomass, EIV moisture, EIV nutrients	iPhND, iPhMD, iPhDD	MPD	-134.8	80.3	0.15
Standing biomass, EIV moisture, EIV nutrients	iPhND, iPhMD	Richness, MPD	-134.4	80.1	0.12
Presence of leaf herbivory					
Standing biomass, EIV moisture, EIV nutrients	iPhMD	Richness, MPD	62.9	-20.4	0.11
		MPD	63.6	-25.8	0.07
Standing biomass, EIV moisture, EIV nutrients	iPhND, iPhMD	Richness, MPD	64.6	-20.3	0.05
Presence of damaged fruits					
	iPhND		146.6	-67.3	0.13
	iPhND, iPhDD		147.2	-66.6	0.10
	iPhMD		147.9	-67.9	0.07

AIC, Akaike Information Criterion; EIV, Ellenberg indicator values.

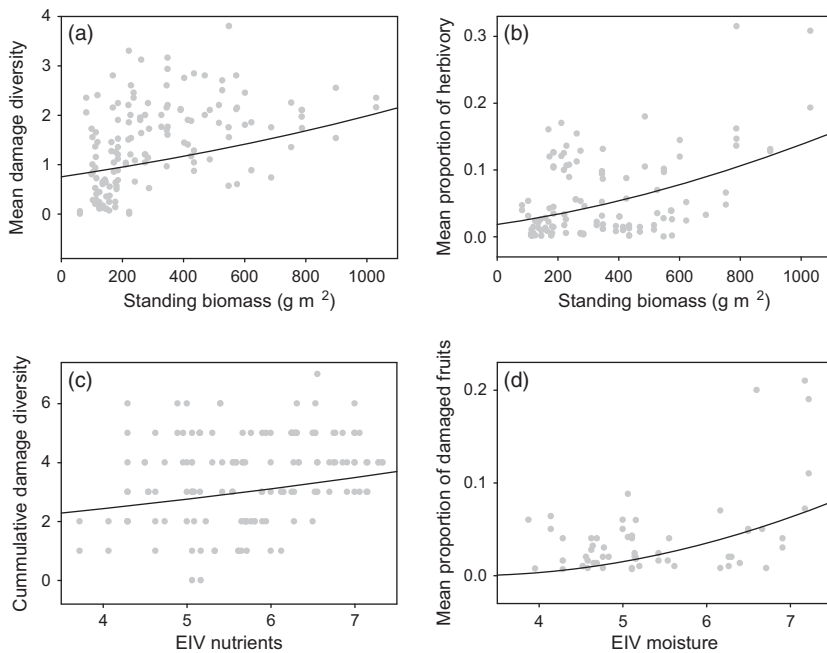


Fig. 1. Effect of habitat fertility on damage diversity and damage levels. Habitat fertility was represented by standing biomass (a, b) and by Ellenberg indicator values (EIV) for nutrients (c) and moisture (d). Symbols indicate individual exotic populations from both 2008 and 2009. The lines are fits to exotic populations from models with the highest Akaike Information Criterion (AIC) weight (see Table 2a).

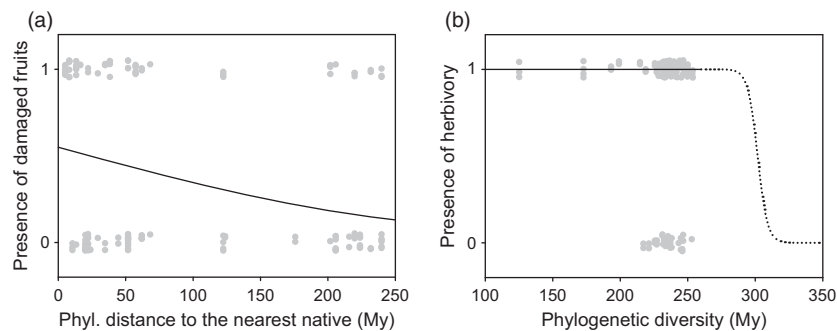


Fig. 2. Effect of phylogenetic distance to the nearest native neighbour (a) and phylogenetic diversity (b) on presence of damaged fruits and herbivory, respectively. Data points were jittered for visibility. In (b), the value range exceeding observed phylogenetic diversity is shown by dotted line. Symbols indicate individual exotic populations from both 2008 and 2009. The lines are fits to exotic populations from models with the highest Akaike Information Criterion (AIC) weight (see Table 2a).

ness predictors appeared more often in the three best models (Table 2b). These results suggest that the effects of relatedness may be nonlinear. Nevertheless, measures of habitat fertility remained the most important predictors (Table 2b and Appendix S7).

The effect of habitat predictors was independent of plant size (canopy height) of exotic species. After canopy height was included in the models, analyses identified the same predictors as the most important determinants of damage diversity and levels as those in models without size as a covariable (Appendix S7).

ERH/R ERH TEST

In 2009, compared with 2008, there were significantly more damage types per individual (1.56 vs. 1.19), a higher propor-

tion of damaged fruits (13.56% vs. 6.67% of damaged fruits on average) and a higher probability of leaf herbivory (74.1% vs. 72.4%; Table 3). In accordance with the results of the analyses of the first part of the study, plants in fertile habitats had on average more damage morphotypes than those from less fertile habitats (Table 3). Species from the *Matricaria* genus, which occurred in the least fertile habitats, accumulated 0.46 damage types per individual or 2.38 damage types per population on average. For the species of *Bidens*, a genus from the most fertile habitats, the same parameters were 3 and 1.75 times larger, respectively.

Native and exotic congeners, however, experienced similar levels of mean damage and damage diversity (Table 3 and Fig. 3). The mean proportion of damaged fruits was lower in exotic species, but this difference was not statistically significant (Table 3). The overall analysis indicated that damage

Table 3 Results of linear mixed models testing for the effects of habitat productivity, species origin and their interaction and year (2008 or 2009) on six measures of damage type diversity and damage levels. Significant predictors (at $P \leq 0.05$) are in bold

Variable	Estimate	SE	<i>t</i> value or Z value	<i>P</i>
Mean damage diversity				
Year	0.117	0.034	3.440	< 0.001
Habitat productivity	0.175	0.073	2.397	0.007
Origin	0.180	0.529	0.341	0.744
Productivity × Origin	-0.037	0.094	-0.399	0.694
Cumulative damage diversity				
Year	0.071	0.050	-1.385	0.149
Habitat productivity	0.239	0.084	2.839	0.032
Origin	0.786	0.587	1.339	0.166
Productivity × Origin	-0.147	0.106	-1.385	0.152
Mean proportion of leaf herbivory				
Year	0.0003	0.013	0.026	0.833
Habitat productivity	0.041	0.033	1.244	0.218
Origin	0.051	0.168	0.304	0.919
Productivity × Origin	-0.008	0.030	-0.269	> 0.99
Mean proportion of damaged fruits				
Year	0.104	0.070	3.221	0.002
Habitat productivity	0.046	0.053	0.885	0.125
Origin	-0.315	0.387	-0.814	0.611
Productivity × Origin	0.081	0.070	1.148	0.333
Presence of leaf herbivory				
Year	9.237	18.959	0.136	0.016
Habitat productivity	20.134	29.581	0.681	< 0.001
Origin	-16.193	118.976	-0.136	> 0.99
Productivity × Origin	2.587	18.959	0.136	> 0.99
Presence of damaged fruits				
Year	-1.152	0.624	-1.846	0.066
Habitat productivity	-1.8139	1.111	-1.631	0.147
Origin	-6.028	8.512	-0.708	0.503
Productivity × Origin	1.126	1.514	0.744	0.485

diversity and damage levels were similar for congeneric pairs from unproductive and from productive habitats (non significant 'Productivity x Origin interaction' in Table 3). However, when we regressed the difference between the native and exotic species, in mean and cumulative damage diversity, against productivity, we found significantly negative relationships for both variables (mean damage diversity: t value -0.84 , P 0.005 ; cumulative damage diversity: t value -2.20 , P 0.001 ; Fig. 4). This indicates that exotic species tended to have lower damage diversity than native species in unproductive habitats but that the opposite was true in productive habitats. The R ERH predicts the opposite pattern.

Discussion

COMMUNITY PREDICTORS OF DAMAGE DIVERSITY AND DAMAGE LEVELS ON EXOTICS

The aim of the first part of our study was to assess the relative importance of different plant community characteristics in influencing the herbivore and pathogen damage experienced by exotic populations. Our results indicated that the process

of gaining herbivores in invaded communities was governed mainly by habitat fertility. The other two factors relatedness to and diversity of the native community also had an effect but were less important characteristics. The community parameters directly affected the damage of exotic plants, independently of differences in plant size.

There are a number of reasons why plants in resource rich habitats suffer more from herbivory and other studies have found similar patterns. Coley (1983) compared herbivory on trees growing in gaps and in understorey of tropical forest and found that leaves of species occurring in gaps where light and nutrients were abundant were grazed six times more rapidly than leaves of species from the understorey where resources were more limiting. Similarly, in synthesized temperate grassland communities, Fraser & Grime (1999) found greater herbivore impact on biomass where soil fertility was experimentally increased than at low soil fertility. A positive relationship between habitat fertility (in our study estimated by productivity and by Ellenberg indicator values) and damage diversity and damage levels might be explained by the growth rate hypothesis (Coley, Bryant & Chapin 1985), that is, by a negative relationship between species growth rate and investments in constitutive herbivore defence (but see Kempel *et al.* 2011). Although we did not measure the growth rate of the exotic species, faster growth can be expected in species from habitats with larger mean indicator values for nutrients (Dostál *et al.* 2013). Another explanation for more damage in fertile environments could be linked to plant quality. Plant quality (nitrogen content) may have increased with fertility, and this could result in increased herbivory (e.g. Throop & Lerdau 2004). Herbivore abundance could also increase with productivity (Chase *et al.* 2000) possibly resulting in larger herbivory rates at high productivity. Our results therefore suggest that the relationship between herbivory and productivity is similar for native and exotic species, although we could not definitely identify the mechanism behind this.

The finding that higher herbivory rates occur in less phylogenetically diverse communities (Fig. 2b) is in accordance with Elton (1958) and Root (1973) who both predicted higher herbivory levels in simple rather than in diverse communities. Our results also agree with those of some experiments using native plants as phytometers: these studies showed a greater benefit of insecticide application to *Centaurea jacea* seedlings when they were planted in monocultures than in polyculture (Nitschke *et al.* 2010) and higher herbivory rates on seedlings transplanted into low as compared to high diversity grassland (Unsicker *et al.* 2006). The observed pattern could be driven either by predators of the herbivorous insects, which should have lower abundance in less diverse communities, or rather by specialized insect herbivores, which are expected to be more abundant in low diversity communities. Other studies have shown that herbivores are often not obligate specialists but feed on related plant species (Novotny *et al.* 2002), which would agree with our finding that plant phylogenetic diversity was generally a better predictor of herbivory than plant species richness.

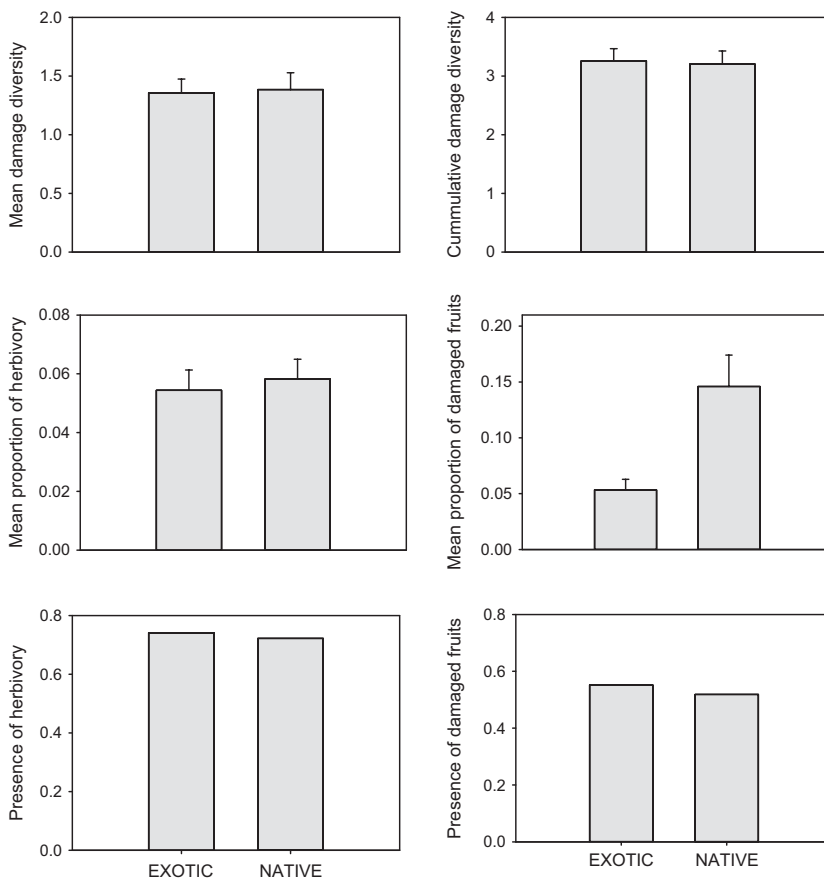


Fig. 3. Damage diversity and damage levels of exotic and native species (mean \pm SE). Data from 2008 and 2009 were pooled. None of the differences were significant at $P < 0.05$.

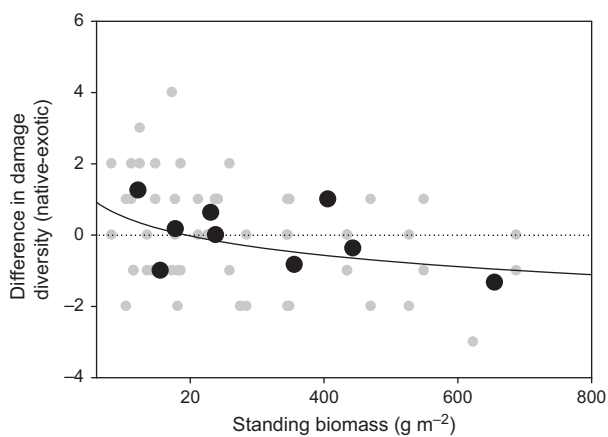


Fig. 4. Difference between native and exotic congeners in cumulative damage diversity plotted against habitat productivity. Small grey symbols indicate congeneric population differences from both 2008 and 2009. Large full symbols indicate mean congeneric differences. The line was fit to the congeneric population differences (small symbols), and the slope was significantly different from zero ($P < 0.001$). Note that the line is nonlinear because the linear model included the natural log of standing biomass.

We found higher rates of fruit damage on exotics growing with more closely related natives, which suggests that oligophagous herbivores were also likely to play a role in the case of pre dispersal fruit damage (Fig. 2a). Such herbivores are primarily confined to native species but are capable of shifting

onto related exotics, as documented in some other studies (e.g. Dawson, Burslem & Hulme 2009; Hill & Kotanen 2009; Ness, Rollinson & Whitney 2011). Our results may therefore support Darwin's naturalization hypothesis, the idea that plant species should find it harder to invade, or to thrive in, communities containing close relatives.

Comparisons of the different community predictors indicated that the nutrient status of the invaded communities is the principal determinant of the intensity of the plant herbivore and plant pathogen interactions. However, because we sampled three plots only per community, estimates of diversity and relatedness may have been imprecise (Gotelli & Ellison 2004). Therefore, although we did not find significant changes in the estimates of diversity and relatedness when we increased the number of sampled plots (see Appendix S3), we cannot rule out the possibility that native diversity and relatedness were falsely identified to be less important predictors of damage on exotics.

Measurement of enemy impact on fitness of exotics and on their demographic performance is a necessary step for the assessment of the spread and impact of these species. Although we have only measured damage caused by plant enemies, there are good reasons to expect that this should be correlated with enemy impact (Mitchell *et al.* 2010). More herbivory, or exposure to more guilds of enemies, was shown to translate into reduced performance, measured by above ground biomass or seed output (e.g. Maron 1998; Rudgers 2004; Puliafico *et al.* 2008). Our results therefore imply that

demographic performance should be reduced more in fertile habitats or in communities containing closely related native species, that is, in those habitats with more herbivory and more damage diversity. However, as herbivore activity some times poorly predicts herbivore control, namely when resource availability also varies (Chase *et al.* 2000; Coupe & Cahill 2003; Cronin, Tonsor & Carson 2010), an experimental approach is needed to examine the differences in exotics' performance in different invaded communities (see also Colautti *et al.* 2004; DeWalt, Denslow & Ickes 2004; Chun, van Kleunen & Dawson 2010; Roy *et al.* 2011). Our observational study is, however, a necessary starting point for such experiments.

ERH/R ERH TEST

The enemy release hypothesis, which assumes that exotic species leave behind more enemies in their native range than they accumulate in the novel range (Torchin & Mitchell 2004), has been a very influential concept in invasion biology. However, here we found no differences in damage diversity and levels between exotic and native congeners growing in the same communities. Even species introduced as recently as 50 years ago, such as *Sedum hispanicum* or *Epilobium ciliatum*, had similar levels of damage as their native relatives, despite the fact that enemy accumulation by exotic species is assumed to be a slow process (Mitchell *et al.* 2010).

Invasive populations in fertile habitats also had similar levels of damage diversity to their native counterparts, which does not support the R ERH (Blumenthal 2005, 2006). Exotic species from fertile habitats may indeed host more enemies at home and lose them during colonization of new ranges (Blumenthal *et al.* 2009); however, these species may also accumulate more biotic interactions in the introduced range. Consequently, our study does not support the R ERH and instead suggests that exotic species can be exposed to similar levels of damage as co occurring native species, irrespective of the habitat productivity.

Several studies showed that exotic species receive less herbivory than native species, thus supporting the ERH (e.g. Agrawal *et al.* 2005; Carpenter & Cappuccino 2005) but many studies did not (reviewed by Colautti *et al.* 2004; Liu & Stiling 2006; Chun, van Kleunen & Dawson 2010). Roy *et al.* (2011) carried out a biogeographical test of the ERH and measured similar traits as we did. Specifically, Roy *et al.* (2011) compared the amount of removed leaf tissue and the frequency of symptoms of 19 different enemy groups on *Brachypodium sylvaticum* in the native (Switzerland) and novel (the USA) ranges. They found total leaf damage to be similar in both ranges. However, leaf damage and symptom frequency due to the different enemy groups differed between ranges. The results of experimental enemy exclusion indicated that a higher intensity of grazing by molluscs and attack by generalist pathogens was likely the reason for the lower performance of *B. sylvaticum* in the native than in the introduced range (Roy *et al.* 2011). Our data indicated a smaller though not statistically significant different proportion of damaged

fruits in populations of exotic than of native species (Fig. 3) with potential consequences for demography of the species.

A possible limitation of our ERH test can be the number of genera included. Although we compared a large number of congeneric population pairs (28 in total), these belonged to a moderate number of genera ($n = 8$) that is rather low in comparison with some previous studies. For instance, Agrawal *et al.* (2005) included 15 genera in their test of the ERH. Our ERH (R ERH) test could also have been too conservative to find lower damage on exotic species (also discussed by Agrawal *et al.* 2005). The first part of our study indicated that fruit damage in populations of exotic species is more likely in the presence of closely related native species (Fig. 2a). Less damage on exotic species than on native congeners might therefore be found for exotics growing without a native congener present. Such congeneric comparisons would, however, be problematic as they could be confounded by potentially different environmental conditions of sites hosting exotic species and sites with native congeners.

We conclude that the ERH and the R ERH do not always explain invasiveness of introduced species. We hypothesize that the invasion success of exotic species, particularly of those from fertile habitats (Hejda *et al.* 2009; van Kleunen, Weber & Fischer 2010; Dostál *et al.* 2013), can be driven by their pre adaptation to the fertile habitats that are becoming increasingly common (Vitousek *et al.* 1997; Tilman *et al.* 2001), rather than by release from negative biotic interactions.

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References

- Agrawal, A.A., Lau, J.A. & Hambäck, P.A. (2006) Community heterogeneity and the evolution of interactions between plants and insect herbivores. *The Quarterly Review of Biology*, **81**, 349–376.
- Agrawal, A.A., Kotanen, P.M., Mitchell, C.E., Power, A.G., Godsoe, W. & Klironomos, J. (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology*, **86**, 2979–2989.
- Baer, S.G., Blair, J.M., Collins, S.L. & Knapp, A.K. (2003) Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology*, **84**, 724–735.
- Bates, D.M. (2010) *lme4: Mixed-effects modeling with R*. Springer.
- Blaney, C.S. & Kotanen, P.M. (2001) Effects of fungal pathogens on seeds of native and exotic plants: a test using congeneric pairs. *Journal of Applied Ecology*, **38**, 1104–1113.
- Blumenthal, D. (2005) Interrelated causes of plant invasion. *Science*, **310**, 243–244.
- Blumenthal, D. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, **9**, 887–895.
- Blumenthal, D., Mitchell, C.E., Pysek, P. & Jarosík, V. (2009) Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences of the USA*, **106**, 7899–7904.

- Carpenter, D. & Cappuccino, N. (2005) Time since introduction and the invasiveness of exotic plants. *Journal of Ecology*, **93**, 315–321.
- Cebrian, J. & Duarte, C.M. (1994) The dependence of herbivory on growth rate in natural plant communities. *Functional Ecology*, **8**, 518–525.
- Chao, A., Colwell, R.K., Lin, C.W. & Gotelli, N.J. (2009) Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, **90**, 1125–1133.
- Chase, J.M., Leibold, M.A., Downing, A.L. & Shurin, J.B. (2000) The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, **81**, 2485–2497.
- Chun, Y.J., van Kleunen, M. & Dawson, W. (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. *Ecology Letters*, **13**, 937–946.
- Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721–733.
- Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.
- Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource availability and plant anti-herbivore defense. *Science*, **230**, 895–899.
- Coupe, M.D. & Cahill, J.F. (2003) Effects of insects on primary production in temperate herbaceous communities: a meta-analysis. *Ecological Entomology*, **28**, 511–521.
- Cronin, J.P., Tonsor, S.J. & Carson, W.P. (2010) A simultaneous test of trophic interaction models: which vegetation characteristic explains herbivore control over plant community mass? *Ecology Letters*, **13**, 202–212.
- Dawson, W., Burslem, D.F.R.P. & Hulme, P.E. (2009) Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions*, **15**, 141–147.
- DeWalt, S.J., Denslow, J.S. & Ickes, K. (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology*, **85**, 471–483.
- Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic and Applied Ecology*, **4**, 493–506.
- Dostál, P. (2010) Post-dispersal seed mortality of exotic and native species: effects of fungal pathogens and seed predators. *Basic and Applied Ecology*, **11**, 676–684.
- Dostál, P. (2011) Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *The American Naturalist*, **177**, 655–667.
- Dostál, P., Dawson, W., van Kleunen, M., Keser, L. & Fischer, M. (2013) Central European plant species from more productive habitats are more invasive at a global scale. *Global Ecology and Biogeography*, **22**, 64–72.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, W., Werner, W. & Paulißen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa [Indicator values of plants in Central Europe]. Ed. 2. *Scripta Geobotanica*, **18**, 1–258.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Endara, M.J. & Coley, P.D. (2011) The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology*, **25**, 389–398.
- Fraser, L.H. & Grime, J.P. (1999) Interacting effects of herbivory and fertility on a synthesized plant community. *Journal of Ecology*, **87**, 514–525.
- Gilbert, G.S. & Webb, C.O. (2007) Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences of the USA*, **104**, 4979–4983.
- Gotelli, N. J. & Ellison, A. M. (2004) *A Primer of Ecological Statistics*. Sinauer and Associates, Sunderland.
- Gujarati, D.N. (1995) *Basic Econometrics*. McGraw-Hill Book Co., Singapore.
- Harvey, K.J., Nipperess, D.A., Britton, D.R. & Hughes, L. (2012) Australian family ties: does a lack of relatives help invasive plants escape natural enemies? *Biological Invasions*, **14**, 2423–2434.
- Hawkes, C.V. (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *The American Naturalist*, **170**, 832–843.
- Hejda, M., Pysek, P., Pergl, J., Sádlo, J., Chytrý, M. & Jarosík, V. (2009) Invasion success of alien plants: do habitat affinities in the native distribution range matter? *Global Ecology and Biogeography*, **18**, 372–382.
- Hill, S.B. & Kotanen, P.M. (2009) Evidence that phylogenetically novel non-indigenous plants experience less herbivory. *Oecologia*, **161**, 581–590.
- Hill, S.B. & Kotanen, P.M. (2011) Phylogenetic structure predicts capitular damage to Asteraceae better than origin or phylogenetic distance to natives. *Oecologia*, **166**, 843–851.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Kempel, A., Schädler, M., Chrobok, T., Fischer, M. & van Kleunen, M. (2011) Trade-offs associated with constitutive and induced plant resistance against herbivory. *Proceedings of the National Academy of Sciences of the USA*, **108**, 5685–5689.
- van Kleunen, M. & Fischer, M. (2009) Release from foliar and floral fungal pathogen species does not explain the geographic spread of naturalized North American plants in Europe. *Journal of Ecology*, **97**, 385–392.
- van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235–245.
- Kleyer, M., Bekker, R.M., Bakker, J., Knevel, I.C., Thompson, K., Sonnenschein, M. et al. (2008) The LEDA Traitbase: a database of plant life-history traits of North West Europe. *Journal of Ecology*, **96**, 1266–1274.
- Lawton, J.H. & Strong, D.R. (1981) Community patterns and competition in folivorous insects. *The American Naturalist*, **118**, 317–338.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.
- Liu, H. & Stiling, P. (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions*, **8**, 1535–1545.
- Maron, J.L. (1998) Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology*, **79**, 1281–1293.
- Maron, J.L. & Vilà, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, **95**, 361–373.
- Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology, Evolution and Systematics*, **11**, 119–161.
- Mitchell, C.E. & Power, A.G. (2003) Release of invasive plants from fungal and viral pathogens. *Nature*, **421**, 625–627.
- Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Huffbauer, R.A., Klironomos, J.N. et al. (2006) Biotic interactions and plant invasions. *Ecology Letters*, **9**, 726–740.
- Mitchell, C.E., Blumenthal, D., Jarosík, V., Puckett, E.E. & Pysek, P. (2010) Controls on pathogen species richness in plants introduced and native ranges: roles of residence time, range size and host traits. *Ecology Letters*, **13**, 1525–1535.
- Ness, J.H., Rollinson, E.J. & Whitney, K.D. (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos*, **120**, 1327–1334.
- Nitschke, N., Ebeling, A., Rottstock, T., Scherber, C., Middelhoff, C., Creutzburg, S., Weigelt, A., Tschamtkke, T., Fischer, M. & Weisser, W.W. (2010) Time course of plant diversity effects on *Centaurea jacea* establishment and the role of competition and herbivory. *Journal of Plant Ecology*, **3**, 109–121.
- Novotny, V., Bassett, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. & Drozd, P. (2002) Low host specificity of herbivorous insects in a tropical forest. *Nature*, **416**, 841–844.
- Parker, I.M. & Gilbert, G.G. (2007) When there is no escape: the effects of natural enemies on native, invasive, and noninvasive plants. *Ecology*, **88**, 1210–1224.
- Poulin, R. & Morand, S. (2004) *Parasite Biodiversity*. Smithsonian Books, Washington, DC.
- Puliafico, K.P., Schwarzlander, M., Harmon, B.L. & Hinz, H.L. (2008) Effect of generalist insect herbivores on introduced *Lepidium draba* (Brassicaceae): implications for the enemy release hypothesis. *Journal of Applied Entomology*, **132**, 519–529.
- Pysek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA*, **94**, 13730–13734.
- Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95–124.
- Roy, B.A., Coulson, T., Blaser, W., Policha, T., Stewart, J.L., Blaisdell, G.K. & Gusewell, S. (2011) Population regulation by enemies of the grass *Brachypodium sylvaticum*: demography in native and invaded ranges. *Ecology*, **92**, 665–675.
- Rudgers, J.A. (2004) Enemies of herbivores can shape plant traits: selection in a facultative ant-plant mutualism. *Ecology*, **85**, 192–205.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M. et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.
- Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.

- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, **152**, 738–750.
- Throop, H.L. & Lerdau, M.T. (2004) Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems*, **7**, 109–133.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281–284.
- Torchin, M.E. & Mitchell, C.E. (2004) Parasites, pathogens, and invasions by plants and animals. *Frontiers in Ecology and the Environment*, **2**, 183–190.
- Unsicker, S.B., Baer, N., Kahmen, A., Wagner, M., Buchmann, N. & Weisser, W. W. (2006) Invertebrate herbivory along a gradient of plant species diversity in extensively managed grasslands. *Oecologia*, **150**, 233–246.
- Vitousek, P.M., Mooney, H.A., Lubchenko, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Wilf, P. & Labandeira, C.C. (1999) Response of plant-insect associations to Paleocene-Eocene warming. *Science*, **284**, 2153–2156.