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Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees

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Summary

1. Exotic tree species are widely used in forest plantations for their often high productivity and performance compared to native trees. However, these advantages may be compromised by herbivore damage.

2. A list of European insect species that have expanded their host range to one of 28 exotic tree species introduced to Europe was compiled from a systematic literature review. The number of successful expansions was analysed using three predictors: (i) phylogenetic relatedness between exotic and European tree species; (ii) area covered by exotic tree species in Europe; and (iii) time since their introduction into Europe.

3. In total, 590 host expansions of native insects to exotic trees were found, mainly of polyphagous species (43%); 25% of the cases reported some type of damage. Bark and wood borers, and defoliators were the dominant guilds.

4. The number of recruited native insect species and cases where major damage occurred was positively correlated with the geographical extent of exotic trees in Europe and the presence of congeneric native trees.

5. *Synthesis and applications*. The use of exotic tree species creates opportunities for native insect herbivores to expand their host range and increase their damage if they are widely planted next to native congeners. Risk assessment studies are recommended when introducing new tree species for forestry plantations. Risk assessments should include trials on susceptibility to any potential damaging organisms in the introduced range.

Key-words: damage, exotic trees, host expansion, host range, native insects, phylogenetic relatedness, plantation forest

Introduction

During the last two centuries, exotic tree species have been widely planted throughout the world, mainly because of their superior growth or wood quality compared with native trees, in order to meet the increasing demand for timber and other forest products (Zobel, Van Wyk & Stahl 1987). A new wave of planting exotic trees is currently taking place, partly in response to the challenges associated with climate change (Canadell & Raupach 2008). In this respect, forest managers search for tree species that are better adapted to new and future climatic conditions or for fast-growing species that are suitable for carbon sequestration or biofuel production (Sims 2003). While planted forests in Europe (excluding the Russian Federation) occupy about 51 million hectares, the proportion of planted forest consisting of introduced tree species was about 17·1% in 2010 (FAO 2010). These planted forests of exotic trees are largely composed of six species:

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Eucalyptus globulus Labill., in the Iberian Peninsula, *Pseudotsuga menziesii* Franco, mainly in France, Poland and Germany, *Robinia pseudoacacia* L., mostly in Hungary and Poland, *Picea sitchensis* Carr., in UK and Ireland, *Pinus contorta* Douglas, in Sweden and *Pinus radiata* D. Don, in Spain. All these exotic species are characterized by fast growth and good wood quality, which contributed to their selection for planting. In addition, tree species planted outside their native range may benefit from the loss of their natural enemies that are largely absent in their introduced range (Keane & Crawley 2002). This release from herbivory typically results in better performance of exotic plants in newly occupied areas, although this pattern may not be universal (Parker *et al.* 2012). Exotic trees may become increasingly exposed to damage by pest insects native to the area in which they have been established (Brockerhoff, Liebhold & Jactel 2006), which may compromise the productivity of exotic tree plantations.

Many studies have compared the relative vulnerability of native and exotic trees to native phytophagous species, with inconsistent results (Bertheau *et al.* 2009; Zas, Moreira & Sampedro 2011; Carrillo-Gavilán *et al.* 2012). In Europe, exotic conifer species such as *P. contorta* (Langström *et al.* 1995), *P. radiata* (Lombardero, Alonso-Rodríguez & Roca-Posada 2012) and *P. sitchensis* (Fraser & Lawton 1994) have experienced major damage by native European pest insects, whereas *P. menziesii* or *Cedrus atlantica* have been virtually immune so far (Roques, Auger-Rozenberg & Boivin 2006). It is generally thought that the establishment of exotic tree species leads to new associations with indigenous herbivores whereby the susceptibility of exotic trees to native pests may be determined by the rate of native insect recruitment and the intrinsic resistance capacity of introduced tree species (Tahvanainen & Niemelä 1987).

Although an increasing body of evidence supports the hypothesis of higher richness of insect herbivores feeding on a given tree species in its native range than in its introduced area, the effect of enemy release on the extent of herbivory is more controversial (Colautti *et al.* 2004; Liu & Stiling 2006; Carrillo-Gavilán *et al.* 2012). The apparent inconsistencies could be due to the fact that the number of herbivore species is not necessarily proportional to the amount of herbivore damage, as a single pest species at high density may cause more damage than multiple species at low density. Furthermore, different types of insects are likely to vary in their ability to colonize tree species with which they have no co-evolutionary history. For example, host-specific insects may be less adapted to exploit new hosts, whereas generalist herbivores may not differentiate or even prefer exotic over native plant species (Bertheau *et al.* 2010; Morrison & Hay 2011; Parker *et al.* 2012).

Several ecological and evolutionary mechanisms may account for the efficiency and persistence of the enemy release effect on exotic plant performance. Phylogenetic distance of the exotic plants from those found on the invaded range is considered to contribute to the extent of enemy release as the dietary niche of insect herbivores is typically restricted to plants which are phylogenetically close (Goßner *et al.* 2009). However, a recent meta-analysis showed that damage to alien plant species may not necessarily depend on their phylogenetic relatedness to native host plants (Chun, van Kleunen & Dawson 2010). Three hypotheses may account for the reduced effect of phylogenetic relatedness between native and exotic species on the share of herbivores. First, closely related plant lineages may evolve in different biotic and abiotic conditions in different parts of the world, which may have resulted in different adaptations to local herbivores according to the geographic mosaics of co-evolution (Thompson 1999). Secondly, the lack of co-evolution with resident herbivores may render exotic plants more vulnerable to new herbivores in the introduced range because they have not been selected on the basis of specific defences (Parker, Burkepile & Hay 2006; Orians & Ward 2010). Further, local adaptation processes may overcome phylogenetic conservatism in shaping host plant traits involved in resistance to insect herbivores, so that alien plant species and natives may be equally susceptible in the introduced range (Goßner *et al.* 2009).

The susceptibility of exotic plants to herbivory also greatly depends on the likelihood of being encountered and colonized by native herbivores (Pearse *et al.* 2013). Four main factors can control encounter frequencies. First, the species richness of insects found on exotic plants increases with the area covered by these introduced plants (Neuvonen & Niemelä 1981): the species–area relationship. Secondly, species richness of insect herbivores is likely to increase with the time since exotic plant introduction, that is the duration of contact between new host plants and potential insect colonizers: the species–time relationship (Strong, McCoy & Rey 1977; White *et al.* 2006; Brändle *et al.* 2008). Thirdly, the abundance of potential colonizers in particular areas could increase the probability of an exotic plant being ‘found’ (Shmida & Wilson 1985). Ultimately, the ability of insects to colonize novel trees depends on their level of host specificity (Fraser & Lawton 1994). Generalist insects are considered superior colonizers since they are often more plastic in their host selection and are better adapted to feeding on a larger range of plants. Generalist insects are also more likely to cause damage on introduced trees as they rarely lose, and sometimes even gain, fitness when they shift to new host trees (Bertheau *et al.* 2010). Nevertheless, we may hypothesize that once tree resistance is overcome, the extent of damage caused by specialist insects might be higher.

In this study, we used a retrospective analysis of past expansions of native European insect species to 28 exotic tree species introduced in Europe to estimate the probability of host colonization and investigate explanatory mechanisms. In particular, we tested the hypotheses that the degree of colonization of exotic trees depends on (i) the presence and abundance of congeneric tree species or on the phylogenetic relatedness between exotics and natives, (ii) the area covered by each exotic tree species, and (iii) the time since their introduction.

We qualified each European insect species found on exotic trees according to its host specificity to investigate the effect of diet breadth on the rate of exotic tree colonization. Further, to address the impact that these host expansions may bring to forest plantations, reported damage was determined for each tree–insect pair. The findings of this large-scale review were used to develop recommendations and relevant criteria for assessing the risk of impact of native phytophagous insects on exotic trees.

Materials and methods

LITERATURE SEARCH

Twenty-eight tree species were identified as exotic in Europe and planted for forestry purposes. A protocol was developed for a systematic review (Pullin & Stewart 2006) of the forest insect species native to Europe which expanded their host range to these introduced trees. The search was constructed from the following terms: (‘Tree Species scientific name’, e.g. *Quercus rubra*, OR ‘Tree Species common name’, e.g. red oak) AND (Europe OR Austria OR Belgium OR Britain OR Croatia OR Czech* OR Denmark OR Finland OR France OR Germany OR Greece OR Hungary OR Ireland OR Italy OR Netherlands OR Norway OR Poland OR Portugal OR Romania OR Scotland OR Serbia OR Spain OR Sweden OR Switzerland OR Turkey OR United Kingdom) AND (insect OR pest OR beetle OR moth OR weevil OR aphid OR scale insect OR gall* OR wasp OR psyllid OR defoliator OR wood borer OR damage) for the insect type. The following electronic data bases were used: CAB abstracts, ISI Web of Science and the first 100 ‘hits’ from scholar.google.com. In addition, queries were made in online Library databases of University of Lisbon. From all the papers obtained, we retrieved as relevant those mentioning any insect herbivore, native to Europe and observed to feed on or use for reproduction one or more of the 28 selected exotic tree species (Fig. 1). We could then determine the number of European native insect species (N_{ins}) which expanded their host range to each exotic tree species.

The number of insect reports on a given tree species is likely to increase with increasing total number of publications on the same tree. To reduce this possible ‘sampling bias’, an additional query in ISI and CAB data bases was conducted to estimate the number of publications mentioning the same exotic tree species in the same geographical areas, regardless of the topic of research. This total number of publications was then used to normalize data on native insects in order to control for a possible ‘sampling bias’ due to particular scientific interest in a given exotic tree, a method used by other studies that analysed comparable publication measures (Ward & Lafferty 2004). Normalized numbers of native insect species that expanded their range on a given exotic tree species ($\mathrm{SN}_{\mathrm{ins}}$) were then obtained as follow:

$$\mathrm{SN}_{\mathrm{ins}}(i) = N_{\mathrm{ins}}(i) \times \frac{\text{Total number of publications reporting native on exotic species}\,(i)}{\text{Total number of publications on exotic tree species}\,(i)}$$

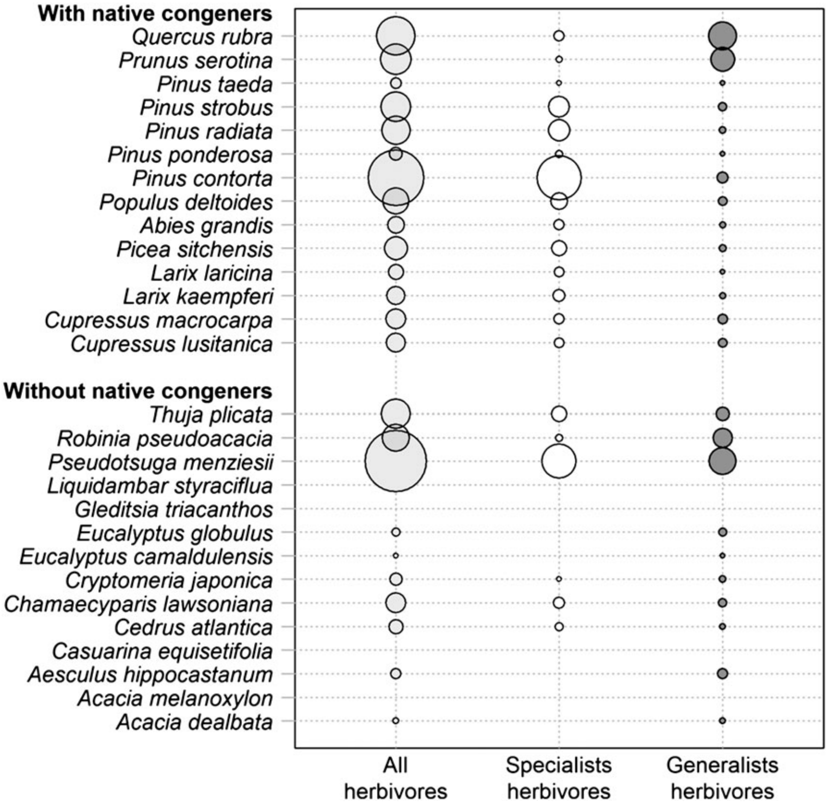

Fig. 1. Relative number of native insect herbivores recruited by exotic tree species introduced in Europe. Dot diameter is proportional to the number of native insect species recruited.

FEEDING CHARACTERISTICS OF HERBIVOROUS INSECTS

Host specificity of native herbivore insects was defined according to two categories: 'generalist herbivores' are those that are able to feed on several host species from different families, and 'specialist herbivores' are those that develop exclusively on hosts within a single genus or family. Although this is a rigid separation, it reflects the fact that the host range of most specialized forest herbivores is restricted to confamilial or congeneric plant species (Novotny & Basset 2005).

Eight feeding guilds were also defined: defoliator, bark borer (e.g. bark beetles feeding on phloem), root borer, wood borer, sap sucker, cone and seed feeder, shoot feeder and gall maker. The part of the tree attacked was defined as roots, stem, foliage, and fruits or seeds (including cones). Host specificity and feeding guild were determined by literature review on each particular insect species retrieved.

Three categories of damage severity caused by insect herbivores were defined according to their impact on trees as reported in the retrieved papers: (i) 'low to moderate damage' – when the authors report damage caused to exotic trees as indicated by tree defoliation, tree mortality or loss of biomass; (ii) 'high damage' – when authors report intense attacks, usually with more than 50% of trees affected; (iii) 'indifferent' – for insects which caused no or little damage, mainly retrieved from papers giving inventory lists of herbivores found associated with one particular tree species or lists of tree species where a particular insect or guild (e.g. xylophagous) was observed without any mention of damage or harmful effect.

AREA COVERED BY INTRODUCED TREE SPECIES

Area planted (hereafter AP) was retrieved from Forest Food and Agriculture Organization of the United Nations (FAO) forestry data bases (FAO 2001 and 2006), for European countries, excluding Russia and the former states of the Soviet Union, the European Forest Institute EFISCEN Inventory Database (Schelhaas *et al.* 2006), and complemented with data from National Forest Inventories (NFI) between 2000 and 2010 for Portugal, Spain, France, Italy, UK and Germany. As NFI report only species planted in large areas within a particular country, data for trees species seldom planted were generally not available. In these cases, it was considered that the planted area occupied <1000 hectares, the smallest unit used in forest inventories. The area planted for a given exotic tree (AP) was calculated as the sum of planted areas across all European countries where this particular tree species is present. To estimate the geographical distribution range (GR) of a given exotic tree in Europe, we considered the countries where the species was planted and estimated the total area covered by these countries.

For each species, we also retrieved the time since first introduction (*T*) in Europe, based on country-specific data about time of introduction.

PHYLOGENETIC DISTANCE BETWEEN INTRODUCED AND NATIVE SPECIES

To test the effect of phylogenetic relatedness between native and introduced species on the probability of colonization by native insects, we first classified introduced species as having or not congeneric species in Europe's native flora (CG). We also calculated the number of congeneric tree species in Europe (NCG). To quantitatively estimate the evolutionary relatedness, we computed a phylogenetic tree including 320 European native and the 28 introduced tree species, using Phylomatic (Webb & Donoghue 2005) and the APG III megatree (Angiosperm Phylogeny Group 2009). Branch lengths (My) were added to the phylogeny using the BLADJ algorithm in Phylocom (Webb, Ackerly & Kembel 2008) and node ages from Wikström, Savolainen & Chase (2001) for angiosperms and Crisp & Cook (2011) for gymnosperms. We used the AGENODE function in Phylomatic to estimate the age of the most recent common ancestor (CA) to each exotic species and its closest native species in Europe.

DATA ANALYSIS

To test whether the abundance of insects' expansions differed among host trees with and without congeners on native European trees, we used chi-square (χ^2) tests. Expected vs. observed frequencies were analysed according to the insect host specificity (generalists vs. specialists) and damage (damaging vs. indifferent insects).

Generalized linear models (GLM) were used to test the effects of the predictors described above on the number of native European pest species that expanded from native to exotic tree species introduced in Europe with a sample size of $n = 28$ (i.e. the number of exotic tree species analysed). We considered as response variables the total number of insect species and the normalized number of insect species that colonized a given exotic tree species (SN_{ins}).

Negative binomial and normal distributions models were used for the total number of insects and the normalized number of insects, respectively.

Several non-independent explanatory variables describing phylogenetic distance between introduced and native tree species (CG, NCG and CA), area of introduction (GR and AP) and time since introduction (*T*) were considered. We tested the following model hypothesis: (i) time alone (T), (ii) geographical range alone (GR or AP), (iii) phylogenetic variables only (CG, NCG or CA); (iv) phylogenetic variables plus geographical range; (v) geographical range plus time; and (vi) phylogenetic variables plus geographical range plus time. The best model, given the data and model set, was identified based on Akaike Information Criterion corrected for small sample size AICc, using differences in AICc scores (Δ_i) and weights w_i (Burnham & Anderson 2002). Model parameters and predictions reported are derived from the best model.

Results

DATA BASE SEARCH RESULTS

A total of 1220 papers were retrieved from ISI and 1529 from CAB, of which only about 8%, 107 and 132, respectively, were relevant for the present study in the sense that they documented information on herbivore insect species native to Europe feeding on one or more of the considered exotic trees introduced in this region. Forty-five relevant papers were common to the two data bases. Relevant papers documenting native insect damage on exotic trees represented about 70%, whereas other type of papers included a list of insect species found on a given tree species and region, or a list of host trees for a given native insect species, family or feeding guild (e.g. wood borers).

NUMBER OF NATIVE INSECTS RECRUITED, HOST SPECIFICITY AND FEEDING GUILDS

In total, 372 insect species native to Europe were found to have expanded their host range to one or more exotic tree species introduced to Europe. When counting insect-tree pairs, 590 host shifts were reported (see Table S1 in Supporting Information). The number of native insects recruited per introduced tree species varied from zero, observed in a few species, for example *Liquidambar styraciflua* (L.), to 94 insect species observed on *P. menziesii* (Table S1, Supporting information, Fig. 1).

Overall, native insects recruited by introduced tree species comprised 45% generalists (i.e. polyphagous) and 55% specialists. Insect specialization and the presence of congeneric tree species were found associated ($\chi^2 = 17{\cdot}82$, $P < 0{\cdot}001$). Specialists were more frequent on exotic trees with European congeners, whereas generalists were more frequent on exotic trees without European congeners (Fig. 1).

Defoliators represented the greatest number of native insects recruited (32%), followed by bark borers (23%) and wood borer species (21%). In contrast, only 1% of the insects were gall makers. Native insect herbivores predominantly attacked foliage (44%) and stems (43%), while attacks to roots (7%), seeds (4%) and shoots (3%) were reported less frequently. Each feeding guild was represented by two or three major families (Fig. 2).

The impact (damage) on exotic trees increased with the presence of congeneric European species. Major damage was reported in only 5% of the cases, always when the exotic trees had congener species, which was identified as a significant factor ($\chi^2 = 18{\cdot}98$, $P < 0{\cdot}001$). Also, 69% of the insect species causing damage were specialists. Most native insects recruited (75%) were 'indifferent', that is they caused no or low damage (Fig. 3).

TESTING ECOLOGICAL DRIVERS OF HOST EXPANSIONS

Both the normalized number of insects and the total number of insects were fitted by several models accounting for the effects of time since introduction, distribution area in Europe and phylogenetic relatedness of the exotic tree with the European ones (Table 1). Focusing on the total number of native herbivorous insects that expanded their host range, the model combining the effects of geographical distribution range (GR) and taxonomic information (the presence of congeneric species, CG) provided the best fit (Table 1). Modelling the total or the normalized number of insects gave similar results: the number of herbivore shifts on introduced trees increased with their distribution area (Fig. 4) and was higher on trees with congeners in the European flora (Table 2).

No other model was within a Δ_i of two units for both response variables (Table 1). Regarding the two area-related variables, the geographical range over which exotic species were planted (GR) received more support than the total area planted in the model selection process (Table 1). The presence of congeneric trees in Europe (CG) was a better indicator than the number of congeneric species (NCG) or the age of the most recent common ancestor (CA) in terms of the normalized number of insect species, whereas for the total number of insect species, CG and NCG were equally indicative (Table 1). Time since introduction was not retained as relevant

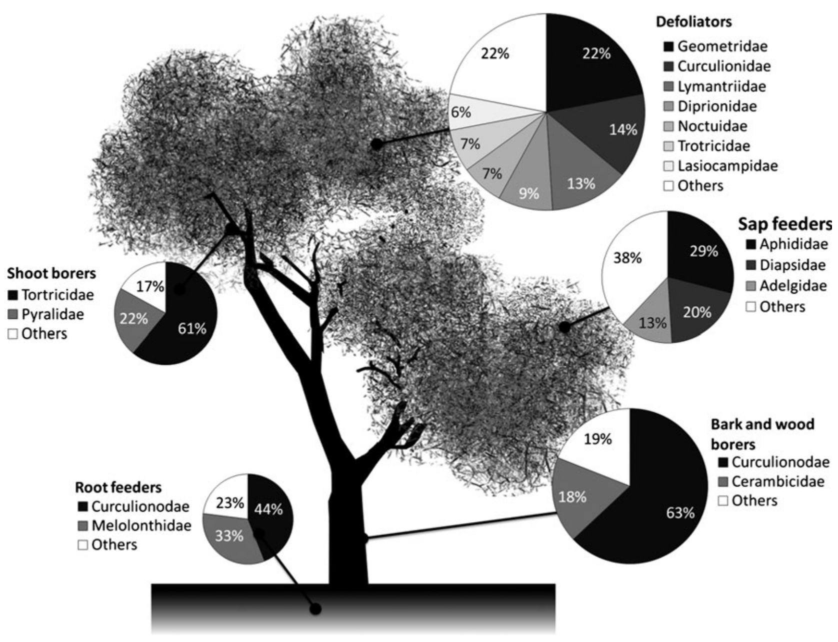

Fig. 2. Feeding guilds and major families of native European insects which expanded their host range to feed on exotic tree species introduced in Europe. The sizes of the circles are proportional to the relative numbers of insects recruited by each feeding guild.

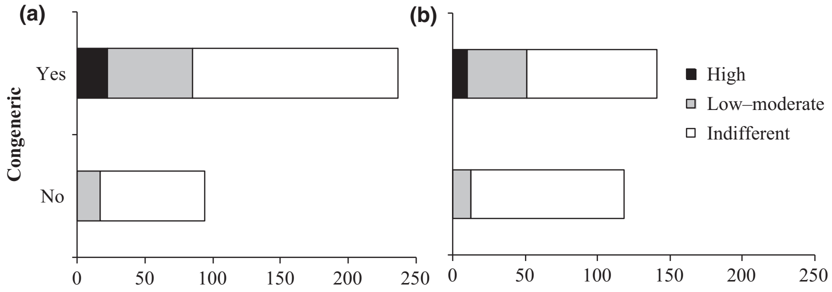

Fig. 3. Number of native European insect recruited according to the presence (yes) or absence (no) of congeneric tree species in Europe grouped in three categories of damage: ‘high’; ‘low–moderate’; and ‘indifferent’ – when no damage is reported, for (a) specialist insects and (b) generalist insects.

Table 1. Summary of models testing the effects of time since introduction (T), area covered (geographical range GR or area planted AP), phylogenetic relatedness (the presence of congeners CG, number of congeners NCG or age of the most common ancestor CA), on the total and the normalized number of native insect herbivores that expanded their host range to exotic tree species in Europe. Normal and binomial negative distributions were considered for the normalized insect species and total insect species response variables, respectively

	Normalized insect species			Total insect species			Specialist insect species			Generalist insect species		
Model variables	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i	AICc	Δ_i	w_i
Intercept only	68·9	9·5	0·01	229·4	9·9	0	199·9	17·0	0	184·8	8·2	0·01
CG	65·9	6·4	0·03	230·4	11·0	0	196·9	14·0	0	187·0	10·3	0
NCG	68·8	9·3	0·01	228·7	9·2	0·01	198·3	15·4	0	183·4	6·7	0·02
CA	71·0	11·5	0	232·7	13·2	0	202·1	19·1	0	186·8	10·2	0
GR	63·4	3·9	0·09	222·6	3·1	0·12	191·1	8·2	0·01	178·9	2·3	0·18
AP	68·5	9·1	0·01	227·2	7·7	0·01	195·1	12·2	0	184·1	7·5	0·01
T	71·5	12·0	0	232·3	12·9	0	202·2	19·2	0	184·3	7·7	0·01
CG + GR	**59·5**	**0**	**0·63**	**219·5**	**0**	**0·57**	**182·9**	**0**	**0·70**	180·7	4·1	0·07
GR + T	66·1	11·5	0	222·5	3·1	0·12	193·5	10·6	0	**176·6**	**0**	**0·55**
CG + GR + T	61·5	2·0	0·23	222·1	2·6	0·16	184·8	1·85	0·28	179·2	2·6	0·15

AICc, Finite sample Akaike Information Criterion; Δ_i, AICc difference between each model and the model with the lowest AICc; w_i, Akaike’s weights.
Bold characters correspond to the best model.

explanatory variable, either considered alone or in multivariate models (Table 1).

The results for insect specialists were similar. The model including times since introduction (*T*) with CG and GR remained within a Δ_i of two units with the best model, but Akaike’s weight was weak ($w_i = 0{\cdot}27$, Table 1). For the insect generalists, the model combining GR and T provided the lowest AICc (Table 1). The presence of congeners (CG) was not a relevant explanatory variable, either considered alone or in multivariate models.

Discussion

In this retrospective analysis, focusing on native insects that attack the main exotic tree species introduced to Europe for forestry purposes, we found almost 400 insect species which were able to broaden their feeding niche by using introduced tree species as new host plants. However, we observed considerable variation in the number of recruited insects among different exotic tree species, and we were able to identify some key factors that account for this. The geographical range covered by exotic tree species and the presence of congeneric species native to Europe emerged as the two main factors explaining these differences.

AREA COVERED BY INTRODUCED TREE SPECIES

The geographical distribution range was the best predictor of the number of native insects recruited by introduced trees. For example, Douglas fir *P. menziesii* is the exotic species most widely planted in Europe and it experienced the highest number of native insect recruitments (more than 90) even though there are no congeneric *Pseudotsuga* species in the region. At the other end of the gradient, only two native insects were found reported for *Pinus taeda* L., which is planted within a small geographical range in Europe, although more than 10 congeneric *Pinus* species are native in Europe. A large range of distribution provides the requisites for novel interactions to occur between a plant and insect herbivores, that is more opportunities of co-occurrence in space (Pearse *et al.* 2013). Systematic comparative studies have consistently reported an increase in the number of insect species with increasing geographical range of the host tree (Neuvonen & Niemelä 1981; Kennedy & Southwood 1984; Leather 1986).

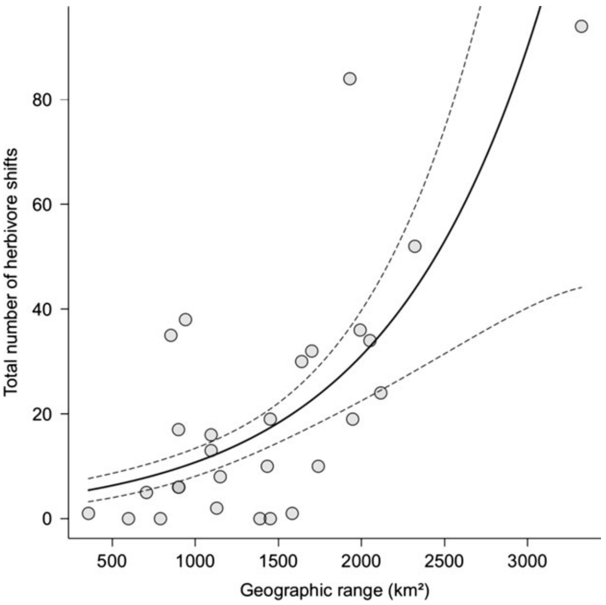

Fig. 4. Effect of the geographical area over which exotic tree species were planted on the total number of native European insect herbivores that expanded their host range to the same exotic tree. Solid and dashed lines represent predictions from model including geographic range (GR) as the only one explanatory variable (log-likelihood ratio test: LR = 9·64, P = 0·002).

However, we should acknowledge that the present result may partly be due to publication bias, as attention from more scientists to particular tree species may occur, either because it occupies larger areas or is economically more relevant. To circumvent this problem, for each introduced tree species, we normalized the number of native herbivores. The raw data and the normalized data both provide consistent results about the importance of geographical range as a main factor, which suggest the lack of bias in estimating the number of insect species that shifted onto exotic trees.

PHYLOGENETIC RELATEDNESS BETWEEN INTRODUCED AND NATIVE SPECIES

Our results also provide evidence for the importance of phylogenetic relatedness of host plants as a factor that promotes the occurrence of host expansions. Several authors pointed out that an exotic plant had to be both abundant and taxonomically close to native hosts to be colonized by native herbivores (Neuvonen & Niemelä 1981; Roques, Auger-Rozenberg & Boivin 2006; Connor *et al.* 2008; Goßner *et al.* 2009). The main mechanism behind the positive relationship between phylogenetic proximity and likelihood of herbivore colonization involving host expansion is that closely related host plants are likely to share functional traits which may be involved either in host plant selection or host resistance (Ricciardi & Ward 2006; Pearse *et al.* 2013).

Again, due to phylogenetic conservatism in traits, damage by novel insect herbivores is expected to decrease with increasing phylogenetic distance between exotic and native plant species (Pearse & Hipp 2009; Harvey *et al.* 2012; Pearse *et al.* 2013). However, in the present study, the age of the most recent common ancestor between exotic and native tree species in Europe (CA) was not a significant predictor of the number of native insects recruited. This finding suggests that time of divergence by itself is not the main factor driving differentiation. The rate of divergence among species is likely to depend on other more important factors such as divergent selective pressures that can occur rapidly in very contrasting environments and result in different adaptations to herbivores (Thompson 1999). The presence/absence of congeneric tree species (CG) better explained the number of host expansions. We observed that not only the number of native forest insects but also their impact (damage) on exotic trees appeared to increase with the presence of congeneric European species (Fig. 3). This may be justified by the fact that plant species of different genera are also highly divergent on many phenotypic traits, including, in particular, those matching the herbivore ability for its recognition and digestion (Pearse *et al.* 2013).

Pseudotsuga menziesii harboured the highest number of recruited insects and has no native congeners in Europe. Based on our review, *P. menziesii* largely shares the same insect herbivores with *Pinus* species native to Europe, representing about 70% of the insects recruited in this species. There could also be legacies of host use based on the occurrence of the phylogenetically close genus *Tsuga* which used to occur in Europe but became extinct during the Pleistocene (Niemelä & Mattson 1996). Nevertheless, the damage observed on *P. menziesii* was low or negligible for 98% of the herbivore species, indicating that, despite

Table 2. Parameter estimates (β), standard errors (SE) and test of effects for the model testing the effects of geographical range (GR) and the presence of congeners (CG) on the total and normalized number of native insect herbivores that expanded their host range to exotic tree species in Europe

	Normalized insect species				Total insect species			
Parameter	β	SE	χ^2	P	β	SE	χ^2	P
CG = 0*	−0·61	0·22	8·70	0·003	−0·04	0·02	4·06	0·043
GR	5·88E^{-04}	1·78E^{-04}	11·51	<0·001	4·33E^{-05}	1·20E^{-05}	13·36	<0·001

*Contrast CG = 1.

colonization, in most cases, *P. menziesii* was not a suitable host or had some level of resistance.

TIME SINCE INTRODUCTION

For specialist insects, our results did not support the hypothesis that the number of recruited species increases with duration of exposure, that is 'species–time hypothesis' (Strong, McCoy & Rey 1977; Kennedy & Southwood 1984; White *et al*. 2006). The fact that the time between the oldest introduction (1640) and the most recent one (1960) in the selected group of trees was relatively small, about 350 years, in terms of historical and especially evolutionary timescales may in part explain the lack of an effect. For example, Kennedy & Southwood (1984) used temporal data for tree species presence spanning the last 13 000 years. Still, for generalist insects, a model combining GR and time provided the best fit, indicating that 'species–time hypothesis' may apply for polyphagous insects within the time frame analysed.

HOST SPECIFICITY AND FEEDING GUILDS

Specialists were particularly frequent on exotic trees with European congeners as reported by Roques, Auger-Rozenberg & Boivin (2006), whereas for generalists, the presence of European congeners was no longer a significant predictor variable. Since diet breadth is wider for generalist herbivores, this may allow a shift onto exotics with no detrimental consequence for fitness (Bertheau *et al*. 2010). Feeding guild recruited by exotic tree species well reflects the insect communities feeding on living trees in temperate forests (Dajoz 1998). Thus, no clear bias for a particular feeding guild emerged from our results. Some feeding guilds, gall makers in particular, were under-represented, which might be due to their high host specialization (Price, Fernandes & Waring 1987).

MANAGEMENT IMPLICATIONS

The present study demonstrates that host expansion by native – and potentially damaging – herbivores may occur more frequently than previously thought, emphasizing the need for a careful evaluation of risk when introducing new tree species for plantation purposes. These results can be used to develop guidelines for the selection of tree species suitable for introduction, for example, to identify alien trees which can be regarded as safe alternatives to native trees in the context of climate change adaptation. Exotic trees species closely related to native trees are particularly prone to damage by local native insects. For example, *P. radiata* plantations are intensively damaged by *Thaumetopoea pityocampa* in southern Europe (Lombardero, Alonso-Rodríguez & Roca-Posada 2012), where it co-occurs with several European pine species. Conversely, *P. radiata* plantations in New Zealand, where no native pines occur, have been remarkably immune to any major pest problem so far. Congeneric species are also prone to other risks such as genetic pollution through hybridization with native species (Mooney & Cleland 2001).

On the other hand, the introduction of exotic trees with no local congeners should also be considered with caution. From a forestry perspective, such species may escape local pests and therefore deliver superior productivity but, from an ecological point of view, their release from natural enemies could enhance their invasiveness, which occurs, for example, in pines planted in the southern hemisphere (Ledgard 2001). Non-native plantings might be also detrimental for biodiversity (Brockerhoff *et al*. 2013).

Thus, we recommend that risk assessments considering several factors including invasiveness, hybridization and susceptibility to native insect species or pathogens be conducted prior to the introduction of exotic trees species for plantation purposes. Introduced tree species should not be planted as large monocultures or in mixtures with closely related species in order to decrease the risk of pest damage (Castagneyrol *et al*. 2014) while maintaining or enhancing productivity (Zhang, Chen & Reich 2012).

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Data accessibility

Tree and insect species description: uploaded as online Supporting information (Table S1).

Data model input file: DRYAD entry http://dx.doi.org/10.5061/dryad.tr61n (Branco *et al*. 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. List of tree-insect species with reported associations of native insect herbivores with exotic tree species in Europe.