ECOLOGY LETTERS

Ecology Letters, (2010) **13**: 506–515 doi: 10.1111/j.1461-0248.2010.01445.x

LETTER

Novel insect-tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness

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Abstract

The translocation of species beyond their native range is a major threat to biodiversity. Invasions by tree-feeding insects attacking native trees and the colonization of introduced trees by native insects result in new insect–tree relationships. To date there is uncertainty about the key factors that influence the outcome of these novel interactions. We report the results of a meta-analysis of 346 pairwise comparisons of forest insect fitness on novel and ancient host tree species from 31 publications. Host specificity of insects and phylogenetic relatedness between ancient and novel host trees emerged as key factors influencing insect fitness. Overall, fitness was significantly lower on novel host species than on ancient hosts. However, in some cases, fitness increased on novel hosts, mainly in polyphagous insects or when close relatives of ancient host trees were colonized. Our synthesis enables greatly improved impact prediction and risk assessment of biological invasions.

Keywords

Fitness, forest, genetic relatedness, host shift, insect, invasion, meta-analysis.

Ecology Letters (2010) 13: 506–515

INTRODUCTION

With the intensification of global trade, the establishment of exotic pest insects affecting trees and other plants has significantly increased in the last decades (e.g. Langor *et al.* 2009; Roques *et al.* 2009), sometimes resulting in widespread, dramatic outbreaks (Lieutier 2006). In North America alone, the Asian longhorned beetle (*Anoplophora glabripennis* Motchulsky) and the emerald ash borer (*Agrilus planipennis* Fairmaire), introduced from Asia and the brown spruce longhorned beetle [*Tetropium fuscum* (F.)], introduced from Asia or Europe, have killed millions of native trees and caused significant environmental and economic impacts (e.g. Colautti *et al.* 2006; Haack *et al.* 2010). Likewise, exotic trees are now widely used in plantation forestry and therefore increasingly exposed to phytophagous insects native to the areas where they have been introduced (Fraser & Lawton 1994; Degomez & Wagner 2001). For example, the European pine processionary moth (*Thaumetopoea pityocampa* Schiff.) causes serious damage to plantations of the North American Monterey pine (*Pinus radiata* D. Don.) (Baraza *et al.* 2007). Although the invasion of tree-feeding insects differs in several aspects from the colonization of introduced trees by native insects, both usually lead to new associations between an insect and a tree; i.e. there has not been any prior experience of these interacting species and there has not been sufficient time for the development of adaptations such as specific defence mechanisms (Gardner & Agrawal 2002).

Several authors have compared the relative susceptibility to native phytophagous insects of novel and ancient host tree species, with conflicting results (e.g. Degomez & Wagner 2001; Dalin & Björkman 2006). For example, it has been suggested that some native European insects perform particularly well and cause major damage, on tree species introduced from North America such as *Pinus contorta* (Långström *et al.* 1995) and *Picea sitchensis* (Fraser & Lawton 1994). By contrast, other exotic trees that are widely planted in Europe, such as *Pseudotsuga menziesii* (native to North America) and *Cedrus atlantica* (native to North Africa), have so far not exhibited any significant damage from native European insects (Lieutier 2006; Roques *et al.* 2006).

Previous attempts to identify factors that predispose tree species to colonization by insects have shed some light on this problem (Lieutier 2006; Mattson *et al.* 2007). The probability of colonization of novel host trees has been found to be correlated with their abundance in the introduced range (e.g. Strong 1974; Neuvonen & Niemelä 1981) or with the duration of their presence (Kennedy & Southwood 1984). An important factor is the lower effect of natural enemies in newly colonized areas. This is due to the fact that most invaders leave their antagonists behind and have acquired fewer new natural enemies. This phenomenon is widely known as the 'enemy release hypothesis' (Keane & Crawley 2002; Colautti *et al.* 2004).

A key factor that applies to both types of new insect–tree associations is the phylogenetic relationship between ancient and novel host tree species. A phytophagous insect is generally expected to preferentially accept novel host trees which are more closely related to its ancient host (Degomez & Wagner 2001; Roques *et al.* 2006) because they are likely to share certain biochemical, morphological and phenological traits that make them similarly acceptable to a particular phytophagous insect (Poore *et al.* 2008). However, in some cases phylogenetically distant plants can have similar secondary compounds which are often involved in determining the host range of insects (Becerra 1997). Ultimately, an insect's ability to colonize a new tree also depends on its level of host specificity which is a strong determinant of which and how many plants can be colonized (Fraser & Lawton 1994). Generalist insects often are more flexible in their host selection and their larvae are better adapted to feeding on a wider range of plants. However, if a novel host tree is closely related to the ancient host of an insect, even a specialist herbivore may extend its host range and colonize the new host (Dalin & Björkman 2006; Lieutier 2006).

Predicting the impact of new insect invaders or of native insects that attack introduced plant species is difficult as this depends on numerous factors that are difficult to disentangle. To date, these factors have mostly been studied by experiments assessing differences in insect abundance or damage on new vs. ancient hosts whereas comparatively little information is available on the effects of host shifting on insect fitness *per se*. Yet, fitness is probably a better estimator of insect adaptation to a new host since it typically indicates the ability to produce viable, abundant and fertile offspring. Therefore, we have conducted a meta-analysis of 346 pairwise comparisons of forest insect fitness on novel and ancient host tree species. The review was restricted to comparisons made in the absence of natural enemies to exclude confounding effects of enemy release and enable a clear focus on direct insect–plant relationships. The results show that, overall, fitness of forest insects is significantly reduced when they are developing on novel host tree species. However, this outcome greatly varies with the phylogenetic relatedness between new and ancient host tree species and with the degree of insect host specificity. These findings provide important information for our understanding of the mechanisms of insect adaptation to novel hosts and for risk assessment of invasive insects and exotic tree plantations.

MATERIALS AND METHODS

Data collection

Published studies that compared the fitness of forest insects on novel vs. ancient host tree species were compiled using bibliographic databases including ISI Web of Science and CAB Abstracts. Keyword searches were conducted using various combinations of relevant terms such as: ('native', 'indigenous', 'local', 'natural' or 'ancient') and ('exotic', 'alien', 'introduced', 'new', 'novel' or 'invasive') and ('insect' or 'pest') and ('tree' or 'forest'). We also surveyed the cited references in relevant articles we retrieved. Studies were included in the meta-analysis if they met the following specific criteria:

(1) The fitness of an insect species was compared between pairs of one ancient and one novel host forest trees. Forest tree species were qualified as 'ancient hosts' if they belong to the host range of an insect species in its native area. For an exotic insect species in a given country, an exotic tree species in the same country was considered as 'ancient host' if it was a host in the native range of the insect. Tree species were qualified as 'novel host' if they were not recorded as ancient hosts in the native area of the insect. In a given country, a novel host could either be an exotic tree that was attacked by a native insect or a native tree attacked by an exotic insect. We considered as fitness variables all measures that quantified fertility, fecundity or the number of surviving progeny of a given female genotype (Henry 2001) or correlated characteristics such as adult or progeny size, weight or feeding efficiency (see the list of retrieved variables in Appendix S1). We excluded studies that reported only on damage or abundance of adult insects during the selection or colonization phase on the host tree because these measures are often indicators of tree resistance and they cannot be transformed into estimates of fitness of individual insects.
(2) The mean of the response (fitness) variable, a measure of the variance (SD, SE, or CI) and the sample size were reported (in the text, tables or graphs) to allow calculation of effect sizes.
(3) The reported paired comparison between novel and ancient host trees was made under the same experi-

mental conditions, on the same date and in the same locality.

Our literature search yielded 412 comparisons of forest insect fitness on novel and ancient host species. Among these, 45 comparisons concerned the test of insect herbivores as potential biocontrol agents of introduced tree species. The selection of biocontrol agents is likely to be biased towards species that exhibited high fitness on the ancient host (in order to be an effective control agent on the target species) and low fitness on novel hosts to avoid any damage to non-target species in the new range. To avoid this potential bias in comparisons of fitness we decided to exclude biocontrol agents from this analysis. There were also 21 comparisons that had been conducted in the potential presence of natural enemies (i.e. in the field and with no protection from insect herbivores). These 21 comparisons were too few to allow testing the effect of enemy release on the fitness of their prey and they were therefore removed from the dataset to restrict the focus on direct insect–tree relationships.

Hence, this meta-analysis is based on 346 pairwise comparisons derived from 31 publications and reports that appeared between 1986 and 2009 (see the list of references in Appendix S2). They involved 24 insect species (Appendix S1) in 19 genera. Of these, 80 cases (23%) focus on a single species (*Lymantria monacha*), two insect genera (*Lymantria* and *Pissodes*) accounted for 47% of the comparisons and the top 10 species accounted for 86%. The main feeding guilds were leaf chewers (66%) and wood borers (31%) which are the most common forest pests but the dataset also included sap feeders (2%) and skeletonizers (1%). A total of 93 tree species from 27 genera and 13 families were studied. Of these, 56% were conifers and 27% were species of the genus *Pinus*. With regard to host shift, 50% comparisons reported on native insect tested on exotic trees and 50% of exotic insects tested on native tree species.

Calculating effect sizes and documenting explanatory variables

The effect of host tree shift on forest insect fitness was estimated by computing Hedges' effect size *d* (Appendix S3). A negative value of *d* indicates lower fitness of forest insects on novel host than on ancient host.

When several fitness variables (response variables) were available, we selected only one variable per comparison between ancient and novel host in order to avoid pseudo-replication. We selected as response variable the variable documented with the largest sample size or the variable that allowed the highest number of possible paired comparisons. When several variables corresponded to several life stages preference was given to using data for the adult stage. When results for a response variable were reported for several years in the same sample we only used data from the first year. When results of an experiment were reported for two years but from two different tree samples, data for each year were used as two separate comparisons. Likewise, two independent experiments (different sites, insects or tree species) reported in the same paper were considered as two separate comparisons.

We split the data set into subsets of classes of different categories of insects and novel hosts trees. Firstly, insects were classified according to their host specificity, whereby those that are host specific within a tree genus were categorized as 'monophagous', those host specific within a tree family were categorized as 'oligophagous', and those that feed on trees from more than one family were categorized as 'polyphagous'. Secondly, for each comparison, the novel host tree species was classified according to its phylogenetic relatedness to the ancient host tree species with which it was compared. We defined three categories: 'SG-SF' if the novel host belonged to the same genus (and therefore also to the same family) as the ancient host, 'DG-SF' if the novel host belonged to a different genus within the same family, and 'DG-DF' if the novel host belonged to a different family (and necessarily to a different genus) than the ancient host.

Furthermore, in the subset of data on *Pinus* species, we defined two categories: 'SC' if the novel host belonged to the same clade as the ancient host pine species and 'DC' if the novel host belonged to a different clade than the ancient host pine species. To define clades of pine species within the genus *Pinus* we calculated genetic distances between the 23 *Pinus* species that were considered in our dataset using the 23 DNA sequences of the matK gene extracted from GenBank (Eckert & Hall 2006 – Appendix S3). We then grouped the ancient and novel *Pinus* host species into three clades according to the neighbour joining phylogenetic reconstruction (Fig. 2a).

The effect of other covariates would have been of interest. For example, the direction of the host shift (exotic insect on native trees vs. native insect on exotic trees) was assessed; however, there were not enough pairwise comparisons to allow hierarchical testing of this effect within each combination of insect specificity × host tree relatedness. For the same reason (of insufficient degrees of freedom) we could not test the effect of insect's feeding guild.

In many cases, several novel host species were compared to the same ancient host species or several ancient hosts to the same novel host within the same publication. This means these particular comparisons are not truly independent. In the case of multiple comparisons, Lipsey & Wilson (2001) and Little *et al.* (2008) recommend to create an average of the publication-level effect sizes to estimate the

mean effect. To conduct this test we used the method proposed by Borenstein *et al.* (2009) for multiple comparisons within a study (Appendix S3). The outcome was almost identical to that obtained with the complete dataset. To keep the maximum of information and benefit from higher statistical power we therefore decided to use the 346 pairwise comparisons.

Effect sizes across all comparisons were combined using the random effects model (Gurevitch & Hedges 1993) to provide the grand mean effect size (d_{++}). The effect was considered as statistically significant if the bootstrap CI, calculated with 9999 iterations, did not bracket zero. The mean effect size (d_{+}) and 95% bias-corrected bootstrap CI were calculated for each class of insect specificity and host tree relatedness. We used a mixed effect model to test the between-classes heterogeneity and evaluated the significance of the class effect (Gurevitch & Hedges 1999). To account for the problem of multiple comparisons we used the more conservative $P = 0.001$ value for statistical significance (Gates 2002). When multiple tests were conducted with the same data set, the resulting P values were assessed against a Bonferroni-adjusted alpha level.

The so-called 'file drawer problem' was addressed by calculating a fail-safe sample size which represents an estimate of the number of non-significant, unpublished or missing studies that would need to be added to the analysis in order to make the overall test of an effect statistically non-significant. The weighted method proposed by Rosenberg (2005) was used to calculate the fail-safe number for our dataset and this number was compared to Rosenthal's conservative critical value of $5n + 10$ (Rosenberg *et al.* 2000), where n is the total number of individual comparisons. In addition we drew and visually assessed normal quantile plots to identify potential publication bias and abnormalities in data structure (Rosenberg *et al.* 2000).

All analyses were carried out using MetaWin 2.0 software (Rosenberg *et al.* 2000).

RESULTS

Our meta-analysis clearly showed that, overall, forest insect fitness is significantly lower on novel host tree species than on ancient host species. The grand mean effect size equalled −0.61 and was significantly different from zero (CI = −0.84 to −0.38; $P < 0.0001$). According to Cohen (1988), an effect size of 0.5–0.8 shows a medium effect (as in this case). The weighted fail-safe sample size was 12 701, thus a much greater value than the conservative critical values of 1740 ($5 \times 346 + 10$), approximately seven times the number of comparisons included in the meta-analysis. Furthermore, the normal quantile plot did not reveal any outliers, with no gap in the lower values of the effect size and no departure from the normal distribution. Thus these results are unlikely to be affected by publication bias.

Effect of insect host specificity

We were able to determine the degree of insect host specificity for all the 346 comparisons we analysed (Appendix S1). Host specificity had a highly significant effect on the difference between insect fitness on ancient and new host trees (d.f. = 2, $Q_B = 46.9$, $P = 0.0001$). For monophagous insects, the mean effect size was −1.25 (a large effect) (Table 1). For oligophagous insects the effect was also negative but medium (−0.48) and for polyphagous insects the effect was smaller again (0.01) and non-significant. Similar results were obtained for the subset of 112 comparisons involving only *Pinus* species (considering 12 different insect species on 23 pine species). The effect of insect host specificity was highly significant ($P = 0.004$). The mean effect size was largest for monophagous insects and only statistically significant for this group (although the sample sizes for oligophagous and polyphagous insects were perhaps too small to determine significant differences). These results unequivocally indicate that the loss in insect fitness on novel host trees increased with insect host specificity, with the highest loss for the most specialized insects (monophagous) and the lowest for the most generalist (polyphagous) species, as expected.

Effect of host tree phylogenetic relatedness

Using the complete dataset we tested the effect of host tree relatedness for each level of insect host specificity. For monophagous insects, the effect of tree relatedness on fitness loss was not significant ($P = 0.05$, against the alpha value of $0.05/3 = 0.017$ after Bonferroni correction). However, the magnitude of the effect size increased consistently with the phylogenetic distance between ancient and novel host trees (Fig. 1). The loss in fitness increased by a factor of 1.5 or 3 when host shifts involved trees from different genera or different families, respectively. For oligophagous insects, tree relatedness significantly affected insect fitness ($P = 0.0001$). The loss in fitness was not significantly different from zero when the host shift occurred within the same genus or family whereas a large, significant effect was observed when the novel host belonged to a different family (Fig. 1). For polyphagous insects the effect of tree relatedness was not significant ($P = 0.78$) and the change in fitness was not significantly different from zero (Fig. 1). Overall, these results indicate that the loss in insect fitness associated with host shifts increased with the phylogenetic distance between novel and ancient hosts. However, this relationship was strongest for specialist species whereas for generalists the phylogenetic

Table 1 Effect of forest insect host specificity on Hedges' effect size

Class variable	Sample size	Hedges' effect size §	Bias corrected bootstrap CI
All tree species $n = 346$, $P = 0.0001$			
Monophagous insects	121	**−1.25**	−1.58 to −0.94
Oligophagous insects	74	**−0.48**	−0.89 to −0.13
Polyphagous insects	151	+0.01	−0.41 to +0.42
Pinus tree species $n = 112$, $P = 0.004$			
Monophagous insects	79	**−1.41**	−1.82 to −1.02
Oligophagous insects	26	−0.12	−0.47 to +0.29
Polyphagous insects	7	−1.04	−3.75 to +0.49

§Values in bold (Hedges' *d* effect size) significantly differ from zero.

distance between host trees needed to be much greater before a significant loss in insect fitness could be observed.

Results for the data subset on *Pinus* trees confirmed this trend. For monophagous insects, there was a significant effect of host tree relatedness on loss in insect fitness ($P = 0.023$, against the alpha of $0.05/2 = 0.025$ after Bonferroni correction). The loss in fitness was greater when the shift occurred between different clades of *Pinus* species than within the same clade (Fig. 2b). For oligophagous insects there was no significant effect of phylogenetic relatedness on fitness ($P = 0.105$). There were not enough data to test the same effect with polyphagous insects.

Occurrence of gains in insect fitness

Although the overall effect size was significantly negative, in some cases insect fitness was significantly higher on novel than on ancient host tree species (this applied to 60 out of 346 comparisons, about 17%). When split according to all nine combinations of the three types of insect host specificity by three types of phylogenetic relatedness between host trees, no cases of gain in fitness were observed for monophagous insects on novel host trees belonging to a different genus or family and neither for oligophagous insects on novel host trees from a different family (Table 2); however, there were few tests in these cells of the contingency table. We observed significant differences in frequency of fitness gains between different levels of insect specificity and host tree relatedness (5000 iterations, $\chi^2 = 41.5$, $P < 0.0001$), although this analysis does not consider the effect size of individual cases. Significant gains in insect fitness are most probable in polyphagous insects, apparently irrespective of the phylogenetic distance between ancient and novel host trees.

DISCUSSION

Most forest insects perform worse on novel host trees

Our review provides the first comprehensive overview of effects of host tree shifts on insect fitness. Host specificity of insects and host–plant phylogenetic relationships emerged as key factors. Our meta-analysis has considerable statistical power because it involved 346 comparisons across 93 tree species and 24 forest insect species from different feeding guilds. Furthermore, the data set was assembled in an objective way, without any observer preference or other bias in data selection that can occur with conventional, narrative reviews. We acknowledge that species in the borers and leaf chewers guilds accounted for more cases than other guilds and that almost a third of the cases involved pine insects. This reflects the distribution of all available data that

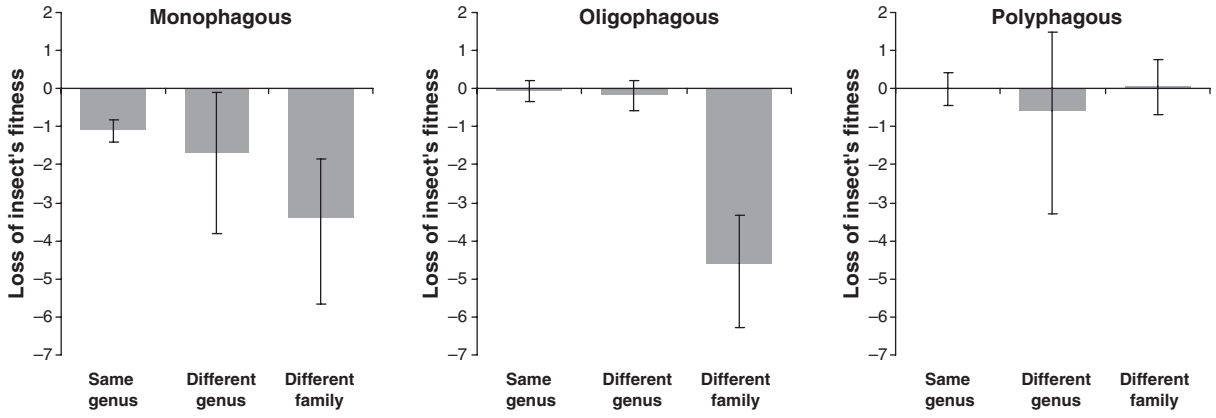

Figure 1 Mean Hedges' effect size ($d \pm 95\%$ bias corrected bootstrap CI) per phylogenetic distance covered during the host shift (within the same tree genus, between different genera of the same family, between two different families) for monophagous, oligophagous and polyphagous insects.

Table 2 Contingency table with the number and proportion of individual comparisons showing significantly positive effect sizes (when an insect's fitness on the novel host tree was greater than on the ancient host, in bold) out of the total number of comparisons for each combination of insect host specificity type × phylogenetic relatedness between ancient and novel host tree. The name of insect species exhibiting significantly higher fitness on novel host trees is shown in italics (in some cases there were several occurrences of the same insect species). A chi-square test with Monte-Carlo procedure (5000 iterations) was performed to compare the proportion of individual comparisons showing significantly positive effect sizes according to insect host specificity (row) and host tree relatedness (column).

	Host trees relatedness			
Insect host specificity	SG-SF	DG-SF	DG-DF	Total
Monophagous	**4**/109 = 4% *Adelges tsugae* *Orthotomicus erosus* *Pineus boerneri*	**0**/7 = 0%	**0**/5 = 0%	**4**/121 = 3%
Oligophagous	**2**/32 = 6% *Pissodes strobi* *Thaumetopoea pityocampa*	**9**/36 = 25% *Dendrolimus sibiricus* *Hylastes ater* *Pissodes strobi*	**0**/6 = 0%	**11**/74 = 15%
Polyphagous	**14**/42 = 33% *Agrilus planipennis* *Nematus pavidus*	**3**/18 = 17% *Lymantria monacha*	**28**/91 = 31% *Lymantria monacha* *Lymantria mathura*	**45**/151 = 30%
Total	**20**/183 = 11%	**12**/61 = 20%	**28**/102 = 27%	**60**/346 = 17%

SG-SF: same genus-same family; DG-SF: different genus-same family; DG-DF: different genus-different family.

are suitable for a meta-analysis and while the substantial number of comparisons provided a robust foundation for our study, some factors (such as feeding guild effects) could not be assessed due to insufficient degrees of freedom. Our literature search revealed numerous other relevant studies that could not be included in the analysis because no adequate statistical information was provided or because the experimental conditions were not sufficiently controlled. Nevertheless, there was a wealth of studies that met the criteria and allowed us to investigate our main questions.

The first striking result of the meta-analysis is that most forest insects lose fitness when they are feeding on a novel host tree. Several authors previously reported on the reduced performance of insects on newly colonized trees planted outside their natural range. For example, attacks by the bark beetle *Tomicus piniperda* in Spain were twice as frequent in stands of *Pinus pinaster* (an ancient host) than on *Pinus radiata* (a novel host) (Lombardero *et al.* 2008). In Sweden, *Ips typographus* is considered to be a major pest on *Picea abies* (ancient host) whereas it is a minor pest on *Pinus contorta* (novel host) (Lindelöw & Björkman 2001). Similar cases have been reported for invading insects that have encountered novel hosts. For instance, larvae of *Anoplophora glabripennis* developed better on Chinese elm (ancient host) than on American elm (novel host) (Bancroft *et al.* 2002). Finally, the horse chestnut leafminer (*Cameraria ohridella*), an invader in Europe, attacks *Acer pseudoplatanus* but it showed considerably lower performance than on its natural host, *Aesculus hippocastanum* (Péré *et al.* 2010).

This general outcome is consistent with reports of higher insect species richness of herbivores and higher levels of herbivory in the native range of invasive plants than in their area of introduction (e.g. Colautti *et al.* 2004) indicating that colonization of novel host plants is not generally a spontaneous process. Interestingly, all these studies showed that generalists are over-represented among insects that are successful colonizers. Similarly, several studies noted that the majority of native insect species that colonized exotic trees are generalist herbivores (Fraser and Lawton 1994; Roques *et al.* 2006). Novotny *et al.* (2003) showed that the probability that a Lepidoptera species colonized alien *Piper* spp. in Papua New Guinea increases from 3% for specialists feeding on a single plant family to 92% for species with a host range greater than 10 families. These findings are consistent with the results of our review which revealed that specialist insects commonly experience greater losses in fitness on novel host trees than generalists.

Are generalist herbivores superior colonizers?

Insect host specificity emerged as a key factor in our review. Not only did generalists experience lower average losses of fitness than specialists (Table 1) they also represented by far the majority of cases where fitness gains occurred (45 out of 60 cases, 75%) (Table 2). These findings suggest the ability of polyphagous insects to develop on novel host trees is related to their tolerance of a wide range of diets or the capacity to withstand various tree defences. The greater

ability of polyphagous insects to colonize, feed and develop on new hosts (Fraser & Lawton 1994; Novotny *et al.* 2003) is probably explained by: (i) the low specificity in host location and oviposition site selection, (ii) the ability to detoxify various allelochemicals, and (iii) larval dispersal behaviours allowing the physical relocation to new hosts that may be more suitable for development (Bernays & Minkenberg 1997). In general, a large proportion of herbivorous insects are specialized on few host plants (Symons & Beccaloni 1999). While this specialization provides fitness increases on certain primary host plants, there is often an associated trade-off, decreased performance on other host plants (e.g. Futuyma 2008). However, recent studies have shown that a wide host range is not necessarily associated with a cost (Friberg & Wiklund 2009), which may explain why some polyphagous species perform equally well on ancient and novel host plants.

Increased susceptibility of congeneric tree species

Plants and their naturally associated herbivores are involved in co-adaptation processes, whereby plants continuously evolve new noxious chemicals as defences while herbivores evolve to overcome these (Schoonhoven *et al.* 2005). In new associations, plants are at an advantage if novel insect associates encounter unfamiliar defences in plants that are phylogenetically distant from their natural hosts, because insects are likely to lack adaptations to these resistance traits (Cappuccino & Arnason 2006). Conversely, introduced plants that experience a significant impact of native herbivores are often closely related to native plants (Louda *et al.* 2003) as successful host shifts in insect herbivores occur more frequently between plants with a close phylogenetic relationship (Janz & Nylin 1998; Lopez-Vaamonde *et al.* 2003). Roques *et al.* (2006) also observed that exotic conifers with native congeners had recruited most of the indigenous insect fauna. These findings are well corroborated by our meta-analysis which indicates decreasing fitness of insects on novel host trees with increasing phylogenetic distance covered during the host shift particularly in monophagous and oligophagous species. In these groups there were also more cases of fitness gain when the new host belonged to the same genus or family, respectively, as the ancient host. This is well illustrated by the example of the European green spruce aphid, *Elatobium abietinum*, which causes more damage on the introduced Sitka spruce than on its ancient host, Norway spruce (Nichols 1987). Predictably, following its introduction to North America, *E. abietinum* has become an important invasive pests on closely related North American spruces, causing considerable damage on Engelmann spruce and blue spruce (Lynch 2004). Another notable case is that of the emerald ash borer (*A. planipennis*) which produces more offspring (and causes far more tree mortality) on North American ash (*Fraxinus* spp.) than its ancient Asian host Manchurian ash (Rebek *et al.* 2008). Other examples that appear to show similar responses are two European invasive monophagous species, *Adelges piceae* and *Cryptococcus fagisuga*, which shifted within the same genus (*Abies* and *Fagus*, respectively) and caused severe damage on North American tree species.

Characteristics of cases of spectacular damage by introduced forest insects and increases of insect fitness

Although our quantitative review clearly shows that, overall, forest insects experience loss of fitness on novel host trees, there are many reports of dramatic damage caused by indigenous pests on exotic trees and by introduced insects on native trees (e.g. Liebhold *et al.* 1995; Brockerhoff *et al.* 2006). Although these reports appear to contradict the outcome of our meta-analysis, the patterns we observed can explain most of these exceptions. First, several of the most polyphagous species are highly damaging introduced pests. These include gypsy moth (*L. dispar*) and Asian longhorned beetle (*A. glabripennis*) which can feed and develop on many different broadleaved trees. Second, high impact species with a narrow host range, such as emerald ash borer (*A. planipennis*) and the pine processionary moth (*T. pityocampa*), have typically colonized novel host trees that are congeneric with their main ancient host trees (see above), where they sometimes experience increases in fitness. Third, besides the direct effects of host plant quality or quantity, several other factors can determine insect performance on novel hosts, which we have not addressed with our analysis. In particular, enemy release is likely to be an important factor. The enemy release hypothesis (ERH) predicts that introduced species are successful because they left their natural enemies behind. This hypothesis has been extensively tested for invasive plants (Keane & Crawley 2002) but not for insects. In fact, only 5% of the studies we reviewed considered this explanation in their interpretation of fitness change on novel host trees. It is likely that in most cases forest pests have been introduced without their specialized (native) natural enemies, that specialist parasitoids of native congenerics experience difficulties to locate and exploit new hosts in the area of introduction and that they are poorly impacted by native generalist predators (three causes of the ERH) (Keane & Crawley 2002).

Towards better prediction of pest insect establishment on novel host trees

Insect specialization and taxonomic proximity between ancient and new host trees clearly are two important predictors of forest insect fitness on novel host trees. We therefore propose to use a combination of these two factors

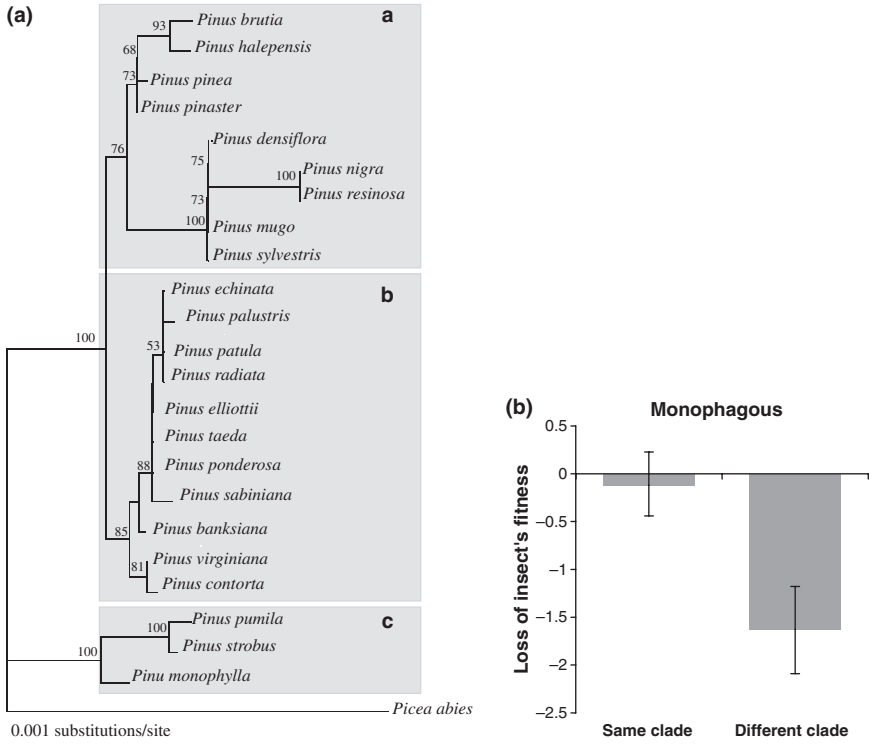

Figure 2 (a) Phylogenetic tree of *Pinus* species included in the meta-analysis showing three clades of species. (b) Mean Hedges' effect size ($d \pm$ bias corrected bootstrap CI) per phylogenetic distance covered during the host shift (within the same clade of pine species, between different clades of pine species) for monophagous insects (species feeding only within the *Pinus* genus).

to assess the potential risk of impact of phytophagous insects on new host trees (Fig. 3). Polyphagous insects are the most likely to become dangerous pests for introduced trees as they rarely lose (and sometimes gain) in fitness when they shifted to new host trees, irrespective of the phylogenetic relationships of the introduced tree with the indigenous flora. For example, there are several such cases affecting large-scale forestry plantings in the UK (Fraser & Lawton 1994). Oligophagous and monophagous insects are expected to pose a lower risk on average, but such insects can perform very well and be extremely damaging, on novel hosts that are closely related to their ancient host. These findings are important for risk assessment considerations regarding the tree species selection for intensive forestry purposes. Exotic trees happen to be widely used in plantation forestry and this trend is likely to increase with

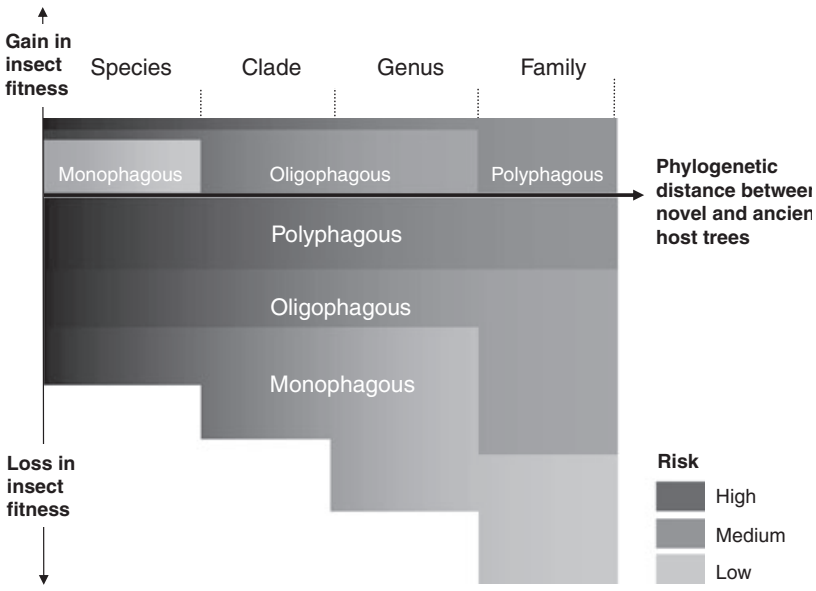

Figure 3 Conceptual diagram showing that the risk of impact due to higher gain or lower loss in forest insect fitness depends on both insect host specificity (higher impact for more generalist species) and phylogenetic distance covered during the host shift (higher impact when the distance between novel and ancient host is short).

incentives for new forest establishment for climate change mitigation and biofuel production. Based on our results, one would expect that introduced tree species that have no taxonomically close relatives in the flora of the introduced region are likely to be the least affected by native insects, particularly those that are mono- or oligophagous. This is indeed the case in New Zealand and several other southern hemisphere countries where *Pinus radiata* and other pines are planted extensively. In the absence of any native Pinaceae in the southern hemisphere, there have been few if any problems with native tree-feeding insects. However, great precautions are necessary to avoid the introduction of specialized insects from the native range of such trees because their release from natural enemies and the lack of competitors means that invaders could be very successful and cause significant damage.

ACKNOWLEDGEMENTS

This work is part of the PhD thesis of C. Bertheau. It was supported by grants from the French Ministry for Agriculture, Fisheries and Rural Affairs (General Directorate of Forests and Rural Affairs) and from the French Ministry of Research and Education. Contributions from E. Brockerhoff were supported by the New Zealand Foundation for Research, Science and Technology through contract C04X0302 (Forest Biosecurity and Protection) and contract C02X0501, the Better Border Biosecurity (B3) programme. We would like to thank Julia Koricheva and three anonymous referees for their helpful comments and advice.

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SUPPORTING INFORMATION

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

Appendix S1 Summary of data included in the meta analyses.
Appendix S2 List of references that have been used to collect data for the meta-analyses.
Appendix S3 Methods to calculate Hedges' effect size, averaged effect size per publication in case of multiple comparisons and genetic distances between pine species.

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Editor, Richard Lindroth
Manuscript received 14 September 2009
First decision made 19 October 2009
Manuscript accepted 11 December 2009