

# Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization

Bastien Castagneyrol<sup>1,2,3\*</sup>, Hervé Jactel<sup>1,2</sup>, Corinne Vacher<sup>1,2</sup>, Eckehard G. Brockerhoff<sup>4</sup> and Julia Koricheva<sup>3</sup>

<sup>1</sup>INRA, UMR 1202 BIOGECO, F-33610 Cestas, France; <sup>2</sup>Univ. Bordeaux, BIOGECO, UMR 1202, F-33400 Talence, France; <sup>3</sup>School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK; and <sup>4</sup>Scion (New Zealand Forest Research Institute), Christchurch 8540, New Zealand

## Summary

1. Pest regulation is an important ecosystem service provided by biodiversity, as plants growing in species-rich communities often experience associational resistance to herbivores. However, little is known about the respective influence of the quantity and identity of associated species on herbivory in focal plants.

2. Using a meta-analysis to compare insect herbivory in pure and mixed forests, we specifically tested the effects of the relative abundance of focal tree species and of phylogenetic distance between focal and associated tree species on the magnitude of associational resistance.

3. Overall, insect herbivory was significantly lower in mixed forests, but the outcome varied greatly depending on the phylogenetic relatedness among tree species and the degree of herbivore feeding specialization.

4. Specialist herbivore damage or abundance was positively related to relative abundance of their host trees, regardless of the phylogenetic distance between host and associated tree species.

5. By contrast, tree diversity triggered associational resistance to generalist herbivores only when tree mixtures included tree species phylogenetically distant to the focal species.

6. *Synthesis and applications.* Our study demonstrates that the establishment of mixed forests *per se* is not sufficient to convey associational resistance to herbivores if the identity of tree species associated in mixtures is not taken into account. As a general rule, mixing phylogenetically more distinct tree species, such as mixtures of conifers and broadleaved trees, results in more effective reduction in herbivore damage.

**Key-words:** associational resistance, forest, herbivores, insects, meta-analysis, pest management, tree diversity

## Introduction

Pest regulation is an important ecosystem service provided by plant diversity. Increasing species richness in plant communities is acknowledged to reduce the risk of insect herbivory experienced by individual plants, a phenomenon known as associational resistance (Jactel & Brockerhoff 2007; Vehviläinen, Koricheva & Ruohomäki 2007; Barbosa *et al.* 2009). However, while climate change is expected to increase the frequency and severity of forest pest outbreaks (Jactel *et al.* 2012; Klapwijk *et al.* 2012), most plantation forests are still managed as single-species stands (Brockerhoff *et al.* 2008). In addition to plant species richness *per se*, species composition of plant assemblages is also a

major determinant of the strength of associational resistance to insect herbivores (Atsatt & Odowd 1976; Scherber *et al.* 2010; Le Guigo, Rolier & Le Corff 2012). In particular, phylogenetic distance between plant species has recently emerged as an important driver of community assembly (Dinnage *et al.* 2012; Mouquet *et al.* 2012) and plant diversity effects on ecosystem functioning (Cadotte, Cardinale & Oakley 2008; Cavender-Bares *et al.* 2009; Flynn *et al.* 2011), but its role in associational resistance to herbivores has seldom been explored (Yguel *et al.* 2011; Gilbert *et al.* 2012). The aim of this study is to evaluate this effect by conducting a meta-analysis of previously published studies on the diversity–herbivore resistance relationship, by focusing on effects of plant phylogenetic diversity rather than plant species richness. Indeed, phylogenetic distance between neighbouring plant species is likely to interfere with the ability of herbivores

\*Correspondence author. E-mail: bastien.castagneyrol@pierreton.inra.fr

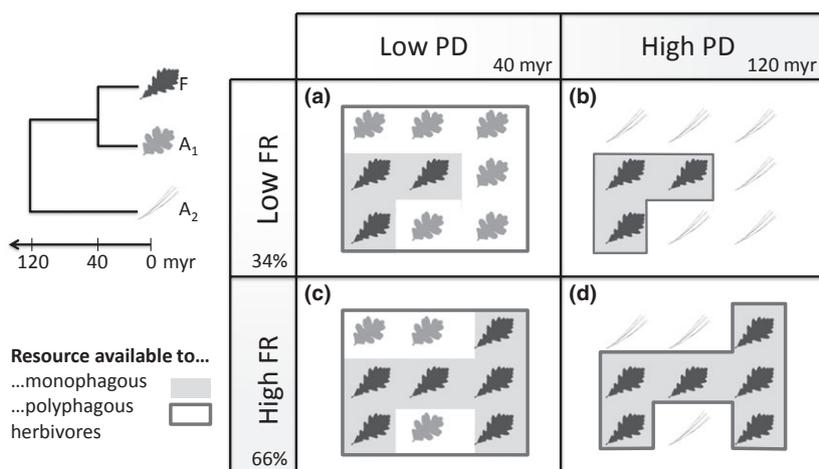
to locate, colonize and exploit their host plants (Yguel *et al.* 2011; Le Guigo, Rolier & Le Corff 2012). This information can improve our understanding of the mechanisms that are responsible for associational resistance to insect herbivores and effectiveness of pest management.

Resource concentration is believed to be one of the main mechanisms underlying associational resistance to insect herbivores (Root 1973; Hambäck, Ågren & Ericson 2000; Björkman *et al.* 2010). The resource concentration hypothesis states that insect herbivores are less likely to find and remain in patches in which their host plant is less likely to be encountered. This may be due to a simple 'host dilution effect' or to physical and chemical masking of the focal plant by heterospecific neighbours (Finch & Collier 2000; Floater & Zalucki 2000; Jactel *et al.* 2011; Dulaurent *et al.* 2012). Masking effects are likely to increase with dissimilarity in the traits used by herbivores to locate and discriminate between host and non-host plants, and the above traits are likely to be more dissimilar as the phylogenetic distance between plant species in the community increases (Gilbert *et al.* 2012; Srivastava *et al.* 2012). There is now growing evidence that the risk of spillover of herbivores from neighbours onto focal plants decreases with the phylogenetic distance between plant species (Ness, Rollinson & Whitney 2011; Gilbert *et al.* 2012; Harvey *et al.* 2012). Moreover, the fitness of herbivores moving from one host to another decreases with taxonomic distance between hosts (Bertheau *et al.* 2010). Such a risk of spillover also depends on the diet breadth of insect herbivores. Most herbivores, even species regarded as 'specialists', are able to feed on several plant species within the same genus (hereafter monophagous) or family (hereafter oligophagous) (Novotny & Basset 2005). This generally results in closely related plant species sharing more herbivore species than more distantly

related plants (Novotny & Basset 2005; Ødegaard, Diserud & Østbye 2005; Pearse & Hipp 2009; Gilbert *et al.* 2012).

For these reasons, we hypothesized that in mixed forests, resistance of a tree species to insect herbivores results from the interplay between three factors: the relative abundance of the focal tree species, the phylogenetic distance between this species and its neighbours, and the degree of insect feeding specialization. To test this hypothesis, we conducted a meta-analysis and compared herbivory (assessed via herbivore abundance or damage caused) by a given insect type (species or feeding guild) on a focal tree species grown as a monoculture with herbivory on the same tree species growing in a mixed stand. We recorded feeding specialization of the herbivore and the percentage of the focal tree species in a mixture and calculated phylogenetic distance between the focal and associated tree species in a mixed stand.

In line with the resource concentration hypothesis (Root 1973), we predicted that mixing focal trees with associated tree species would result in a decrease in frequency of resource available to herbivores in mixed forests, and therefore in stronger associational resistance. Because resource availability is likely to depend on both herbivore feeding specialization and relatedness among tree species (Fig. 1), we distinguished between two types of resources (Fig. 1): the *focal resource* (i.e. the relative abundance of the focal tree species) and the *total resource* (the abundance of both focal tree species and phylogenetically related associated tree species that herbivores are likely to feed on). Our meta-analysis thus expands the resource concentration hypothesis by including phylogenetic information on associated plant species. It also goes beyond the previous meta-analyses on forest diversity effects on herbivores by Vehviläinen, Koricheva &



**Fig. 1.** Conceptual diagram representing the relationship between herbivore specialization, Focal Resource availability (FR) and Phylogenetic Distance (PD) between focal (F) and associated ( $A_1$ ,  $A_2$ ) species. Resource available to monophagous herbivores is the focal resource only (FR). For polyphagous herbivores, tree species associated with the focal resource may be used as alternative resource (a and c) or not (b and d), depending on their phylogenetic relatedness, making total resource potentially available to herbivores a function of both FR and PD. Associational resistance provided by tree diversity is therefore expected to be stronger and more consistent for monophagous than for polyphagous herbivores.

Ruohomäki (2007) and Jactel & Brockerhoff (2007), which were focused on the effect of plant species richness on herbivory damage and did not specifically address the effect of the composition of plant species assemblages.

## Materials and methods

### DATA COLLECTION

We surveyed all studies included in previous meta-analyses on effects of forest diversity on insect herbivory, covering a period from 1960 to 2006 (Jactel & Brockerhoff 2007; Vehviläinen, Koricheva & Ruohomäki 2007) and searched for new studies published between 2006 and 2012. Keyword searches were conducted using various combinations of relevant terms such as: (pure or monoculture) and (mixed or mixture or admixture or mixing) and (forest or stand or plantation) and (insect or pest or Lepidoptera or Coleoptera or Hemiptera). We also surveyed the cited references in relevant articles we retrieved. Studies were retained if they met the following conditions: (i) insect herbivore damage or abundance on a particular tree species (hereafter referred to as the 'focal' species) was compared in pure vs. mixed forest stands in the same area and time period; (ii) the mean of response variable (herbivore damage or abundance), a measure of the variance and the sample size were reported in the text or available from graphs; (iii) identity and relative abundance of tree species in mixed stands were reported. Increase in tree species richness within a stand generally coincides with a decrease in relative abundance of each individual tree species (including the focal tree species), that is, resource dilution. To separate effects of tree species richness from those of resource dilution, we retained only case studies that compared single-species stands with two-species mixtures, which constituted the majority of available data.

Case studies reporting data on tree mortality instead of herbivore abundance or damage were excluded because tree mortality may have resulted from factors other than herbivory and could not be unambiguously attributed to a given herbivore, and because tree mortality may have changed host tree dilution or the composition of mixed stands.

### EFFECT SIZE CALCULATION

For each case study, we calculated effect size as the log of the ratio between the mean of observed herbivore damage or abundance in the mixture ( $M_x$ , treatment) and the mean of observed herbivore damage or abundance in the corresponding monoculture ( $M_0$ , control):  $\log(M_x/M_0)$ . Positive values indicated that herbivory was higher in mixture than in monoculture (i.e. associational susceptibility) while negative effect sizes indicated associational resistance. Log response ratio was back-transformed [ $100 - 100 \times (e^{\log(M_x/M_0)})$ ] to provide a direct estimate of the magnitude of tree mixture effect as percentage decrease or increase in insect herbivory in mixtures as compared to monocultures. Effect sizes and their corresponding variances were calculated in R using the *metafor* package (Viechtbauer 2010; R Core Team 2012).

### HERBIVORE SPECIALIZATION

Insect herbivores were classified according to their diet breadth as monophagous (feeding on hosts restricted to a single plant

genus), oligophagous (feeding on different host genera within a single family) or polyphagous (feeding on different host families). When information on herbivore feeding specialization could not be retrieved from the original study or additional sources, the case studies were included only in the overall assessment of forest diversity effects on herbivores.

### CALCULATING FOCAL AND TOTAL RESOURCE AVAILABILITY

The focal resource availability (FR) was directly extracted from original papers and expressed as the percentage of focal trees in mixtures. Total resource availability (TR) was calculated by combining FR and the phylogenetic distance between focal and associated trees.

To calculate phylogenetic distance between tree species in a mixture, we computed a phylogenetic tree including all the tree species included in the meta-analysis using Phylomatic (Webb, Ackerly & Kembel 2008) and the APG III megatree (Bremer *et al.* 2009). Branch lengths (Myr) were added to the phylogeny using the BLADJ algorithm in Phylocom (Webb, Ackerly & Kembel 2008) and were based on node ages from Wikström, Savolainen & Chase (2001) and Crisp & Cook (2011).

Total resource availability was estimated as:

$$TR = FR + AR \quad \text{eqn 1}$$

where FR is the focal resource availability (i.e. the relative abundance of the focal tree species in the mixture) and AR is the contribution of the associated species to total resource, that is, associated resource availability, estimated as:

$$AR = \sum_i S_i \times A_i \quad \text{eqn 2}$$

where  $A_i$  is the relative abundance of associated species  $A_i$  in the mixture and  $S_i$  is the probability that the focal tree species F shares insect herbivores with the associated tree species  $A_i$ , given their phylogenetic distance ( $PD_{F,A_i}$ ).

$S_i$  was estimated using the relationship and the coefficients  $\beta_0$  and  $\beta_1$  given by Gilbert *et al.* (2012) for insects:

$$S_i = \frac{e^{\beta_0 + \beta_1 \times \log_{10}(1 + PD_{F,A_i})}}{1 + e^{\beta_0 + \beta_1 \times \log_{10}(1 + PD_{F,A_i})}} \quad \text{eqn 3}$$

### STATISTICAL ANALYSES

Many studies included into our meta-analysis provided more than one effect size (e.g. data on herbivory by several insects with different feeding specializations or comparison of pure stands with mixtures containing different percentages of associated tree species). These effect sizes originating from a single study cannot be considered statistically independent, introducing possible errors in confidence interval estimates (Nakagawa & Santos 2012). To account for the potential non-independence, we used linear mixed models (Nakagawa & Santos 2012) with the study level as a random factor. The *lme* function in the *nlme* package in R (Pinheiro *et al.* 2011) was used to test the significance of grand mean effect size and explanatory variables.

We tested FR and TR as continuous variables with meta-regression, and their effects were expressed as slope values. The

best predictor variable was identified based on Akaike Information Criterion (AIC) using the maximum likelihood method. Each model was then reverted to restricted maximum likelihood (REML) so that effect size estimates could be used to compare models describing the same output variable, but with different moderators (Zuur *et al.* 2009).

The final data set was composed of 83 case studies from 22 different publications, with 27, 24 and 21 case studies for monophagous, oligophagous and polyphagous herbivores, respectively (Table S1, in Supporting Information). Information on herbivore specialization was unavailable for 11 case studies.

#### PUBLICATION BIAS

All case studies for oligo- and polyphagous herbivores referred to herbivore damage, while in the monophagous subset, 18 case studies of 28 reported data on insect abundance. To avoid any bias, we tested the difference in mean effect sizes in monophagous herbivores depending on the metric used as a proxy for herbivory. We found no significant differences ( $F_{1,9} = 0.76$ ,  $P = 0.405$ ), and data on abundance and damage were then pooled for subsequent analysis.

We checked for publication bias using funnel plot and trim and fill procedures (Fig. S2, Supporting Information) on the whole data set and on each subset, corresponding to the three levels of host specialization (Borenstein *et al.* 2009). Correcting mean effect sizes for possible publication bias did not change results qualitatively (Table 1). In addition, Rosenberg's fail safe number (Rosenberg 2005) was 3499, thus a much greater value than Rosenthal's critical conservative value ( $5 \times 87 + 10 = 445$ ). The above two tests indicate that our results are robust to publication bias, and asymmetry in the funnel plot (Fig. S2, Supporting Information) may be due to heterogeneity among effect sizes (e.g. due to true differences between herbivore types). We further checked for the presence of outliers using Cleveland dotplots. In the monophagous data set, one case study was identified as an outlier and was removed from the analysis.

## Results

The grand mean effect size calculated on the whole data set was significantly negative (Table 1), corresponding to about 30% decrease in herbivory in mixed stands as compared to monocultures. However, the magnitude of

the effect varied among studies ( $Q = 239.13$ ,  $P < 0.001$ ), suggesting the existence of significant sources of variation.

We tested the effect of moderators (Focal [FR, %] and Total [TR, %] resource relative availability, and herbivore specialization) on effect size, using mixed effect models. FR and TR were strongly correlated ( $r = 0.95$ ), see Fig. S1, Supporting Information) and consequently could not be included in the same model (Graham 2003). We therefore set up two separate models, including as moderators either FR or TR, in addition to the herbivore feeding specialization and the interaction term. We found a significant interaction between herbivore specialization and TR (log-likelihood ratio [LLR] = 8.98,  $P = 0.011$ ), indicating that effects of tree phylogenetic diversity on herbivory varied with herbivore feeding specialization. There was also a significant interaction between host specialization and FR (LLR = 6.63,  $P = 0.036$ ). To better understand the effect of host specialization, we therefore analysed separately the response of mono-, oligo- and polyphagous herbivores to focal and total resource availability.

Monophagous herbivores showed the strongest associational resistance in mixed stands (Fig. 2a, Table 1), with a mean effect size corresponding to a 42% decrease in herbivore abundance or damage in two-species mixtures as compared to pure stands. Oligophagous herbivores showed a weaker but still significant 15% decrease in herbivory in mixed stands (Fig. 2b). Responses of polyphagous herbivores to tree species mixtures were very variable (Fig. 2c) and not significant overall (Table 1).

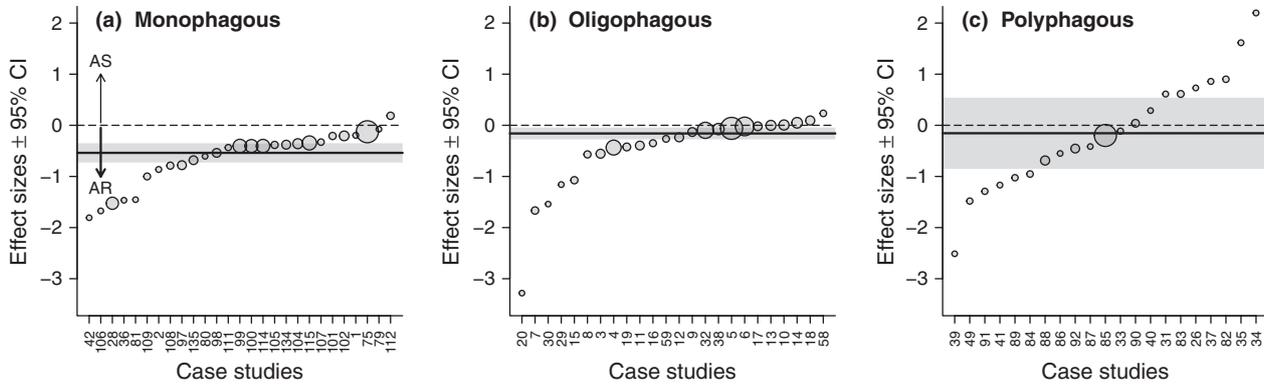
The magnitude of associational resistance to monophagous herbivores decreased with increasing FR ( $F_{1,15} = 4.72$ ,  $P = 0.046$ , Fig. 3a), indicating that focal trees benefited more from being grown in mixtures when their abundance was low compared with the associated species. A similar but weaker trend was observed for TR, but this effect was only marginally significant ( $F_{1,15} = 4.06$ ,  $P = 0.062$ , Fig. 3b and Table S2, Supporting Information).

Both FR ( $F_{1,18} = 32.89$ ,  $P < 0.001$ ) and TR ( $F_{1,18} = 32.52$ ,  $P < 0.001$ ) had significant effects on the responses of oligophagous herbivores to mixed forests (Fig. 3b and e). These effects were slightly stronger (steeper slope) when phylogenetic distance between tree species

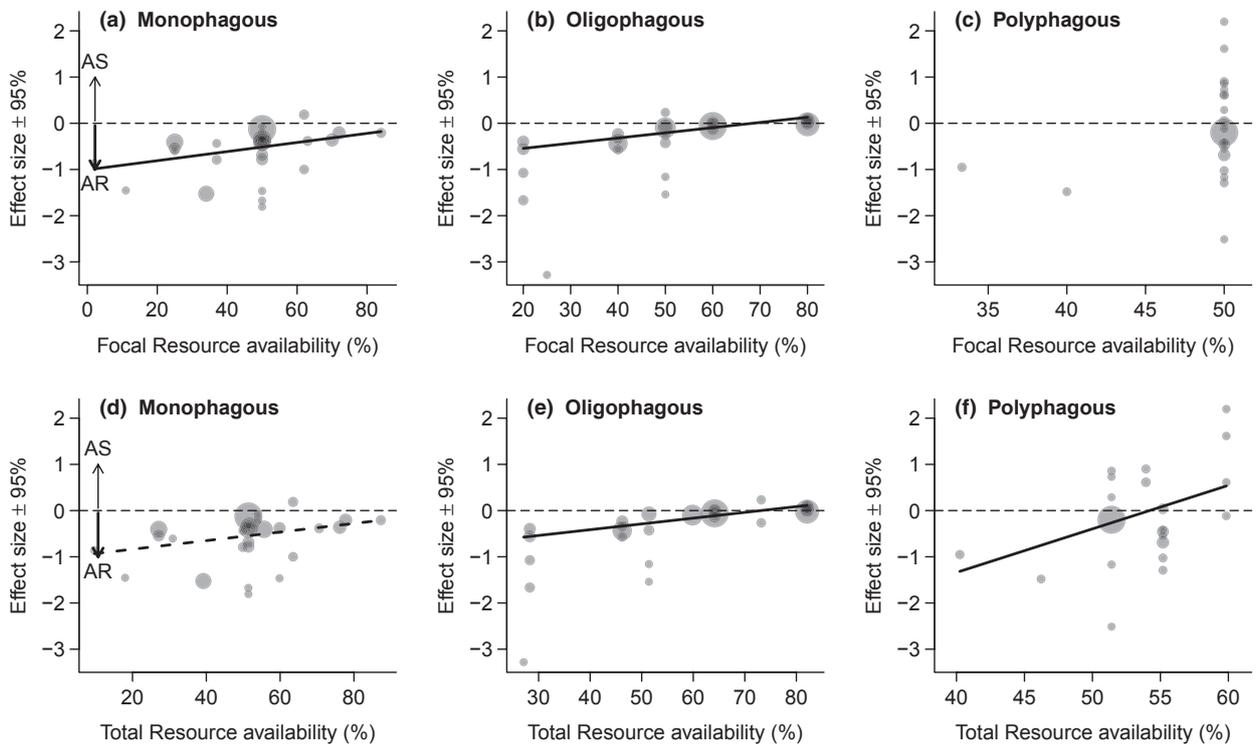
**Table 1.** Summary of mean effect sizes and tests of publication bias. Bold numbers indicate significant associational resistance

	Observed mean effect size ( $\pm 95\%$ CI)	% decrease in herbivory in mixed forests ( $\pm 95\%$ CI)	Bias-corrected mean effect size ( $\pm 95\%$ CI)*	Rosenberg's fail safe number
Complete data set ( $n = 83$ )	<b>-0.36 (-0.56, -0.16)</b>	<b>30.3 (14.60, 43.00)</b>	<b>-0.18 (-0.33, -0.04)</b>	3353
Monophagous ( $n = 27$ )	<b>-0.54 (-0.73, -0.35)</b>	<b>41.7 (29.60, 51.70)</b>	<b>-0.49 (-0.66, -0.32)</b>	628
Oligophagous ( $n = 24$ )	<b>-0.16 (-0.28, -0.04)</b>	<b>14.8 (4.3, 24.0)</b>	<b>-0.27 (-0.43, -0.10)</b>	102
Polyphagous ( $n = 21$ )	-0.16 (-0.85, 0.54)	14.4 (-71.6, 57.3)	-0.05 (-0.51, 0.40)	112

\*Bias-corrected mean effect size corresponds to the mean effect sizes estimated after trim and fill procedure, that is, correcting asymmetry in funnel plot to account for possible missing case studies.



**Fig. 2.** Differences in insect herbivory between pure forest stands and two-species mixtures. Each dot represents an individual effect size for (a) monophagous, (b) oligophagous and (c) polyphagous insect herbivores. Negative effect sizes indicate associational resistance, positive effects indicate associational susceptibility. Dot size is proportional to the weight given to each individual case (inverse of variance). Solid lines and shaded areas are for mean effect sizes and their corresponding 95% confidence intervals. Thin and thick arrows indicate direction of associational susceptibility (AS) and associational resistance (AR), respectively.



**Fig. 3.** Effects of Focal (a–c) and Total Resource availability (d–f) on insect herbivory response to tree diversity for (a and d) mono-, (b and e) oligo- and (c and f) polyphagous herbivores. Horizontal dashed lines represent null effect sizes. Thin and thick arrows indicate direction of associational susceptibility (AS) and associational resistance (AR), respectively. Dot size is proportional to the weight of each individual effect size (inverse of variance). Solid regression lines represent significant effects. Dashed regression lines are for non-significant trends.

was accounted for (i.e. for TR) but comparable in terms of AIC score (Table S2, Supporting Information), indicating that both moderators were equally important.

For polyphagous herbivores, 19 of 21 cases represented equal mixtures of focal and associated species (Fig. 3c), so that the effect of FR on herbivory could not be properly tested. However, the responses of polyphagous herbivores to tree species mixtures significantly depended on TR ( $F_{1,13} = 5.52$ ,  $P = 0.035$ , Table S2, Supporting Information), with a switch from associational susceptibility to

associational resistance when TR was lower than 54% (Fig. 3d). In addition, the effect of TR on herbivory was nine times greater for polyphagous than monophagous or oligophagous herbivores (Fig. 3 and Table S2, Supporting Information).

### Discussion

Our study clearly demonstrates that the relative abundance of the host tree species, its phylogenetic distance to

associated tree species and herbivore specialization are three important factors that have to be considered simultaneously to explain the magnitude and direction of the effect of tree diversity on herbivory regulation.

Decrease in herbivore abundance and damage in mixed stands resulting from associational resistance did emerge as a very general pattern. This is consistent with previous results (Jactel & Brockerhoff 2007), but this overall mean effect is likely to hide differences between herbivores responsible for this damage (Vehviläinen, Koricheva & Ruohomäki 2007). We showed that herbivory by monophagous insect herbivores was reduced in mixed forests more than herbivory by oligophagous herbivores and that the effect of tree diversity on polyphagous herbivores was much more variable and not significant (Fig. 2). While previous meta-analyses mainly focused on species richness or taxonomic diversity (Jactel & Brockerhoff 2007; Vehviläinen, Koricheva & Ruohomäki 2007; Barbosa *et al.* 2009), we made a step further by testing mechanisms responsible for such differences. Here, we confirmed that resource availability is a major driver of the herbivory response to plant diversity, as associational resistance increased with the dilution of the focal tree species, but we showed that accounting for phylogenetic distance between focal and associated species is critical to understanding the magnitude and outcomes of tree diversity effects on insect herbivory. While monophagous herbivores were mainly sensitive to the relative abundance of focal trees (FR), oligo- and polyphagous herbivores were also sensitive to the relative abundance of both focal and closely phylogenetically related host species (TR).

#### PHYLOGENETIC RESOURCE DILUTION: A NEW MECHANISM UNDERLYING THE DIVERSITY-RESISTANCE RELATIONSHIP

In our study, we incorporated information about phylogenetic distance between plant species into the framework of the resource concentration hypothesis to propose a synthetic index of resource availability (namely TR), accounting for both the quantity (relative abundance) and the quality (phylogenetic distance between the focal and possibly alternative host species) of feeding resources. There is indeed a growing body of evidence in the literature, mainly from the field of biological invasions, suggesting higher risk of herbivore damage on focal plants associated with phylogenetically more closely related neighbours (Pearse & Hipp 2009; Ness, Rollinson & Whitney 2011; Gilbert *et al.* 2012; Harvey *et al.* 2012; Parker *et al.* 2012). The main mechanism behind this relationship is that closely related host plants are more likely to share functional traits involved in host recognition and exploitation (Gómez, Verdú & Perfectti 2010; Wiens *et al.* 2010) and are therefore more prone to share common herbivores (Ødegaard, Diserud & Østbye 2005; Weiblen *et al.* 2006).

However, previous studies focusing on forest insects did not try to disentangle the effects of phylogenetic distance

between tree species from those of resource availability for herbivores (Yguel *et al.* 2011). The resource concentration hypothesis has received considerable support (e.g. Hambäck, Ågren & Ericson 2000; Vehviläinen *et al.* 2006; Sholes 2008; Björkman *et al.* 2010). In our meta-analysis, the observation that associational resistance to monophagous and oligophagous herbivores increased with decreasing relative abundance of focal host trees also supports this hypothesis. This may be explained by herbivores experiencing increasing difficulty to find and reach their host plants as their concentration decreases, at both the forest stand and local neighbourhood of focal trees (Hambäck & Beckerman 2003). The main mechanisms behind this are the lower probability of encounter, as well as the disruption of cues that are used for host finding, including physical (Floater & Zalucki 2000; Dulaurent *et al.* 2012) or chemical cues (Jactel *et al.* 2011) emitted by the host plants. For herbivores feeding on a narrow range of closely related plant species, host dilution by other plant species directly results in a decrease in resource availability, whatever the identity of neighbouring plants is (Fig. 1). This is consistent with our result that phylogenetic distance between tree species in mixed forests hardly provides any additional explanation to the response of monophagous herbivores to the focal resource dilution (Fig. 3).

However, to apply the resource concentration hypothesis to more generalist herbivores, one has to take into account all alternative feeding resources. In particular, for oligophagous and polyphagous herbivores, feeding resource availability may remain constant despite a strong decrease in the abundance of the focal host species if associated species can also be used as alternative hosts (Fig. 1a vs. 1c). We observed a consistent switch from associational susceptibility to associational resistance to generalist herbivores as the phylogenetic distance increased between focal and associated trees (Fig. 3f), which is likely to explain the lack of an overall effect of tree diversity on polyphagous herbivores (Fig. 2c).

Although associational resistance was the most common pattern, we did observe associational susceptibility in some cases. This was particularly frequent with polyphagous herbivores in mixed stands containing phylogenetically close tree species (i.e. when  $PD_{A,F}$  was low, Fig. 3f). This result is probably due to spillover of herbivores from preferred associated trees onto less preferred focal trees in mixed stands (White & Whitham 2000). Alternatively, the 'resource dilution hypothesis' posits that herbivore loads per plant may be higher where the density of their hosts is low (Otway, Hector & Lawton 2005), and herbivores may have concentrated on more preferred focal trees when associated with less preferred alternative hosts, also resulting in associational susceptibility. In addition, polyphagous herbivores are known to benefit from feeding on several species rather than on just one host plant (Unsicker *et al.* 2008; Lefcheck *et al.* 2013). This phenomenon, known as diet mixing, may also explain the associational susceptibility

observed when phylogenetic resource dilution was low. Better knowledge of generalist herbivores' preferences for alternative host species will be of interest to evaluate the likelihood of 'phylogenetic dilution' vs. 'spillover' processes for a given composition of mixed forest.

#### CONCLUSIONS AND APPLIED PERSPECTIVES: PROS AND CONS OF MIXED FORESTS

Current forest management needs to be adapted to maintain ecosystem services in the context of major ongoing environmental changes. Several recent syntheses have demonstrated the benefits of mixed forests, compared with monocultures, in terms of productivity (Piotto 2008; Paquette & Messier 2011; Zhang, Chen & Reich 2012), resistance to herbivores (Jactel & Brockerhoff 2007), windthrow (Griess *et al.* 2012) and, more generally, multifunctionality (Gamfeldt *et al.* 2013). However, our study shows that the establishment of mixed forests *per se* is not sufficient to convey resistance to herbivores if the identity of tree species associated in mixtures is not taken into account.

Phylogenetic information is increasingly used by ecologists to unravel mechanisms underlying the diversity–ecosystem functioning relationship (Mouquet *et al.* 2012) and recently emerged as a promising proxy for risk assessment (Gilbert *et al.* 2012) and forest management (Schweizer, Gilbert & Holl 2013). Our findings suggest that it could also be used to design more sustainable and resistant plantation forests. Although mixing closely related tree species could be easier because of their similar habitat and management requirements, our results show that it may lead to higher susceptibility of the focal species to generalist herbivore damage. Our results suggest that increasing the phylogenetic distance between focal and associated tree species is likely to be a better management strategy, because this also provides increased resistance to herbivores, which may compensate for additional costs associated with mixed planting (Nichols, Bristow & Vanclay 2006). In addition, benefits of phylogenetically diverse forests may not be limited to resistance to herbivores (Yguel *et al.* 2011), but also include other ecosystem services. For instance, it has been recently shown that overyielding (i.e. increased production of biomass in mixtures than expected from monocultures) was greater in assemblages of phylogenetically distant plants than of closely related ones (Cadotte 2013). Cost-benefit analyses are therefore needed to find the best compromise in tree species composition to improve the provision of various ecosystem services by mixed forests (Knocke *et al.* 2007).

#### Acknowledgements

The research reported here was conducted as part of the BACCARA and FunDivEurope projects, which received funding from the European Commission's Seventh Framework Programme (FP7/ 2007–2013) under Grant Agreement Nos. 226299 and 265171, respectively. B.C.'s postdoctoral research was funded by the FunDivEurope project. Contributions

by E.B. were supported by core funding from the New Zealand Government to Scion, via the Better Border Biosecurity Collaboration.

#### Author's contributions

HJ initially conceived the study, which evolved significantly with the help of all co-authors. JK, HJ and EGB provided initial data and updated them. CV and BC computed phylogenetic diversity indices. BC conducted the meta-analysis and wrote the paper. All four co-authors reviewed and improved the manuscript.

#### References

- Atsatt, P.R. & Odowd, D.J. (1976) Plant defense guilds. *Science*, **193**, 24–29.
- Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. (2009) Associational resistance and associational susceptibility: having right or wrong neighbours. *Annual Review of Ecology and Systematics*, **40**, 1–20.
- Bertheau, C., Brockerhoff, E.G., Roux-Morabito, G., Lieutier, F. & Jactel, H. (2010) Novel insect–tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness. *Ecology Letters*, **13**, 506–515.
- Björkman, M., Hambäck, P.A., Hopkins, R.J. & Rämert, B. (2010) Evaluating the enemies hypothesis in a clover–cabbage intercrop: effects of generalist and specialist natural enemies on the turnip root fly (*Delia floralis*). *Agricultural and Forest Entomology*, **12**, 123–132.
- Borenstein, M., Hedges, L.V., Higgins, J.P.T. & Rothstein, H.R. (2009) *Introduction to Meta-Analysis*. John Wiley & Sons Ltd., Chichester, UK.
- Bremer, B., Bremer, K., Chase, M.W., Fay, M.F., Reveal, J.L., Soltis, D. *et al.* (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.
- Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C. & Sayer, J. (2008) Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation*, **17**, 925–951.
- Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences*, **105**, 17012–17017.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Crisp, M.D. & Cook, L.G. (2011) Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. *New Phytologist*, **192**, 997–1009.
- Dinnage, R., Cadotte, M.W., Haddad, N.M., Crutsinger, G.M. & Tilman, D. (2012) Diversity of plant evolutionary lineages promotes arthropod diversity (ed D Hooper). *Ecology Letters*, **15**, 1308–1317.
- Dulaurent, A.-M., Porté, A.J., van Halder, I., Vétillard, F., Ménassieu, P. & Jactel, H. (2012) Hide and seek in forests: colonization by the pine processionary moth is impeded by the presence of nonhost trees. *Agricultural and Forest Entomology*, **14**, 19–27.
- Finch, S. & Collier, R.H. (2000) Host-plant selection by insects: a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis Et Applicata*, **96**, 91–102.
- Floater, G.J. & Zalucki, M.P. (2000) Habitat structure and egg distributions in the processionary caterpillar *Ochrogaster lunifer*: lessons for conservation and pest management. *Journal of Applied Ecology*, **37**, 87–99.
- Flynn, D.F.B., Mirotnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011) Functional and phylogenetic diversity as predictors of biodiversity–ecosystem function relationships. *Ecology*, **92**, 1573–1581.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P. *et al.* (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, **4**, 1340.
- Gilbert, G.S., Magarey, R., Suiter, K. & Webb, C.O. (2012) Evolutionary tools for phytosanitary risk analysis: phylogenetic signal as a predictor of host range of plant pests and pathogens. *Evolutionary Applications*, **5**, 869–878.
- Gómez, J.M., Verdú, M. & Perfectti, F. (2010) Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, **465**, 918–921.

- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology*, **84**, 2809–2815.
- Griess, V.C., Acevedo, R., Härtl, F., Staupendahl, K. & Knoke, T. (2012) Does mixing tree species enhance stand resistance against natural hazards? A case study for spruce. *Forest Ecology and Management*, **267**, 284–296.
- Hambäck, P.A., Ågren, J. & Ericson, L. (2000) Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology*, **81**, 1784–1794.
- Hambäck, P.A. & Beckerman, A.P. (2003) Herbivory and plant resource competition: a review of two interacting interactions. *Oikos*, **101**, 26–37.
- 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.
- Jactel, H. & Brockerhoff, E.G. (2007) Tree diversity reduces herbivory by forest insects. *Ecology Letters*, **10**, 835–848.
- Jactel, H., Birgersson, G., Andersson, S. & Schlyter, F. (2011) Non-host volatiles mediate associational resistance to the pine processionary moth. *Oecologia*, **166**, 703–711.
- Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A. & Koricheva, J. (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*, **18**, 267–276.
- Klapwijk, M.J., Ayres, M.P., Battisti, A. & Larsson, S. (2012) Assessing the impact of climate change on outbreak potential. *Insect Outbreaks Revisited* (eds P. Barbosa, D.K. Letourneau & A.A. Agrawal), pp. 429–450. John Wiley & Sons, Ltd, Chichester, UK.
- Knoke, T., Ammer, C., Stimm, B. & Mosandl, R. (2007) Admixing broad-leaved to coniferous tree species: a review on yield, ecological stability and economics. *European Journal of Forest Research*, **127**, 89–101.
- Le Guigo, P., Rolier, A. & Le Corff, J. (2012) Plant neighbourhood influences colonization of Brassicaceae by specialist and generalist aphids. *Oecologia*, **169**, 753–761.
- Lefcheck, J.S., Whalen, M.A., Davenport, T.M., Stone, J.P. & Duffy, J.E. (2013) Physiological effects of diet mixing on consumer fitness: a meta-analysis. *Ecology*, **94**, 565–572.
- Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J. *et al.* (2012) Ecophylogenetics: advances and perspectives. *Biological Reviews*, **87**, 769–785.
- Nakagawa, S. & Santos, E.S.A. (2012) Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, **26**, 1253–1274.
- Ness, J.H., Rollinson, E.J. & Whitney, K.D. (2011) Phylogenetic distance can predict susceptibility to attack by natural enemies. *Oikos*, **120**, 1327–1334.
- Nichols, J.D., Bristow, M. & Vanclay, J.K. (2006) Mixed-species plantations: prospects and challenges. *Forest Ecology and Management*, **233**, 383–390.
- Novotny, V. & Basset, Y. (2005) Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1083–1090.
- Ødegaard, F., Diserud, O.H. & Østbye, K. (2005) The importance of plant relatedness for host utilization among phytophagous insects. *Ecology Letters*, **8**, 612–617.
- Otway, S.J., Hector, A. & Lawton, J.H. (2005) Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology*, **74**, 234–240.
- Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.
- Parker, J.D., Burkepile, D.E., Lajeunesse, M.J. & Lind, E.M. (2012) Phylogenetic isolation increases plant success despite increasing susceptibility to generalist herbivores. *Diversity and Distributions*, **18**, 1–9.
- Pearse, I.S. & Hipp, A.L. (2009) Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. *Proceedings of the National Academy of Sciences*, **106**, 18097–18102.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. & the R Development Core Team. (2011) nlme: Linear and nonlinear mixed effects models, R package version 3.1-102.
- Piotto, D. (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and Management*, **255**, 781–786.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- 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.
- Rosenberg, M.S. (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, **59**, 464–468.
- Scherber, C., Heimann, J., Kohler, G., Mitschunas, N. & Weisser, W.W. (2010) Functional identity versus species richness: herbivory resistance in plant communities. *Oecologia*, **163**, 707–717.
- Schweizer, D., Gilbert, G.S. & Holl, K.D. (2013) Phylogenetic ecology applied to enrichment planting of tropical native tree species. *Forest Ecology and Management*, **297**, 57–66.
- Sholes, O.D.V. (2008) Effects of associational resistance and host density on woodland insect herbivores. *Journal of Animal Ecology*, **77**, 16–23.
- Srivastava, D.S., Cadotte, M.W., MacDonald, A.A.M., Marushia, R.G. & Mirochnick, N. (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters*, **15**, 637–648.
- Unsicker, S., Oswald, A., Köhler, G. & Weisser, W. (2008) Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia*, **156**, 313–324.
- Vehviläinen, H., Koricheva, J. & Ruohomäki, K. (2007) Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. *Oecologia*, **152**, 287–298.
- Vehviläinen, H., Koricheva, J., Ruohomäki, K., Johansson, T. & Valkonen, S. (2006) Effects of tree stand species composition on insect herbivory of silver birch in boreal forests. *Basic and Applied Ecology*, **7**, 1–11.
- Viechtbauer, W. (2010) Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, **36**, 1–48.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.
- Weiblen, G.D., Webb, C.O., Novotny, V., Basset, Y. & Miller, S.E. (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology*, **87**, 62–75.
- White, J.A. & Whitham, T.G. (2000) Associational susceptibility of cottonwood to a box elder herbivore. *Ecology*, **81**, 1795–1803.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V. *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.
- Wikström, N., Savolainen, V. & Chase, M.W. (2001) Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London Series B: Biological Sciences*, **268**, 2211–2220.
- Yguel, B., Bailey, R., Tosh, N.D., Vialatte, A., Vasseur, C., Vitrac, X., Jean, F. & Prinzing, A. (2011) Phytophagy on phylogenetically isolated trees: why hosts should escape their relatives. *Ecology Letters*, **14**, 1117–1124.
- Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology*, **100**, 742–749.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY.

Received 16 April 2013; accepted 16 September 2013

Handling Editor: Marc Cadotte

## Supporting Information

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

**Fig. S1.** Relationship between focal and total resource relative availability.

**Fig. S2.** Funnel plot assessing publication bias for the whole data set.

**Table S1.** Raw data used in analyses

**Table S2.** Summary of meta-regressions of effect sizes against focal and total resource relative availability.

**Appendix 1.** List of references included in the meta-analysis.