

## Species richness of herbivorous insects on *Nothofagus* trees in South America and New Zealand: The importance of chemical attributes of the host

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### Abstract

Several studies have evaluated the relative contribution of various host-plant attributes to the species richness of the associated insect herbivores, with and without the inclusion of the phylogeny of the host species for Northern hemisphere trees. In general these studies reached the same conclusion: tree availability (range and abundance) was a good predictor of insect species richness, although chemical attributes of the trees were not tested. The present study evaluates the relative contribution of ecological attributes of host-plant species within the Southern hemisphere genus *Nothofagus*, to the species richness of their associated insect fauna in South America and New Zealand. The variables included were: area of distribution (*a*), including longitudinal (rln) and latitudinal ranges (rlt), architectural complexity (*c*) and phytochemical attributes of the species, including chemical diversity (*d*) and chemical uniqueness (*u*). The analysis by independent contrasts revealed that the latitudinal range is an important factor, which explained the insect richness associated with *Nothofagus* for all guilds and taxonomic orders, except for the sap feeders. Compared to the non-phylogenetic analyses, including host-plant phylogeny led to the inclusion of additional variables in the regression equations. Phytochemical uniqueness of the host plants was an important factor to explain insect species richness. For example, *Nothofagus alessandrii*, the species with the most unique chemistry, had very few and mostly specialised herbivores, whereas *Nothofagus dombeyi*, with the least unique chemistry, had the highest number of related insect species. We conclude that, in addition to geographic range and phylogenetic relatedness, studies of insect herbivore diversity must also examine plant chemical composition.

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## Zusammenfassung

In mehreren Untersuchungen wurde der relative Beitrag der verschiedenen Eigenschaften von Wirtspflanzen auf die Artenvielfalt der assoziierten herbivoren Insekten bestimmt. Dies geschah unter und ohne Berücksichtigung der Phylogenie der Wirtsarten für Bäume der nördlichen Hemisphäre. Im Allgemeinen kamen diese Untersuchungen zum gleichen Schluss: die Verfügbarkeit der Bäume (Verbreitung und Häufigkeit) war ein guter Indikator der Artenvielfalt von Insekten, obwohl die chemischen Eigenschaften der Bäume nicht untersucht wurden. Die vorliegende Untersuchung bestimmt den relativen Beitrag der ökologischen Eigenschaften der Wirtspflanzenarten zur Artenvielfalt der assoziierten Insektenfauna innerhalb der in der südlichen Hemisphäre verbreiteten Gattung *Nothofagus* in Südamerika und Neuseeland. Die berücksichtigten Variablen waren: Verbreitungsareal ( $a$ ), einschließlich der Verbreitung in Bezug auf die Längengrade ( $rln$ ) und Breitengrade ( $rlt$ ), die architektonische Komplexität ( $c$ ) und phytochemischen Eigenschaften einschließlich der chemischen Diversität ( $d$ ) und der chemischen Einzigartigkeit ( $u$ ). Die Analyse durch unabhängige Vergleiche ließ erkennen, dass die Verbreitung in Bezug auf die Breitengrade einen wichtigen Faktor darstellt, der die Artenvielfalt der Insekten, die mit *Nothofagus* assoziiert sind, für alle Gilden und taxonomischen Ordnungen mit Ausnahme der saugenden Herbivoren erklärt. Im Vergleich zu Analysen ohne Berücksichtigung der Phylogenie führte die Berücksichtigung der Phylogenie der Wirtspflanzen zur Einbeziehung von zusätzlichen Variablen in die Regressionsgleichungen. Die phytochemische Einzigartigkeit der Wirtspflanzen war ein wichtiger Faktor, der die Artenvielfalt der Insekten erklärt. So hatte z. B. *Nothofagus alessandrii*, die Art mit der einzigartigsten Chemie, nur wenige und meistens spezialisierte Herbivore, während *Nothofagus dombeyi*, mit einer wenig einzigartigen Chemie, die größte Anzahl verwandter Insektenarten hatte. Wir schließen daraus, dass Untersuchungen der Diversität herbivorer Insekten zusätzlich zur geographischen Verbreitung und der phylogenetischen Verwandtschaft die chemischen Zusammensetzungen berücksichtigen müssen.

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**Keywords:** Chemical uniqueness; Phylogeny; Latitudinal ranges; Longitudinal ranges; Insect herbivores

## Introduction

Patterns of herbivore diversity on plants are explained by multiple causes (Lewinsohn, Prado, Jordano, Bascompte, & Olesen, 2006). Several studies have evaluated the relative contribution of various attributes of the host plants (e.g. area of distribution, chemical isolation and architectural complexity; for definitions see Methods section below) on the species richness of associated insect herbivores (Basset & Burckhardt, 1992; Cornell, 1985, 1986; Hatcher, 1994; Jones & Lawton, 1991; Lawton & Price, 1979; Lawton & Schroder, 1977; Leather, 1986). The main result of these studies has been that the area of distribution of the host plants has a major influence on the species richness of phytophagous insects and mites (Jones & Lawton 1991; Leather, 1986). The associated herbivore species richness may be attributed not only to ecological factors but also to the phylogenetic relationships of the host plants. Failure to include the phylogenetic relationships of the host plants may lead to erroneous explanations about the adaptive patterns of their associated insects (Brooks & McLennan, 1991). Early studies included “taxonomic isolation” as a variable of the host plants, i.e. the number of host-plant species in the same family or genus to determine its relevance in explaining the number of associated insect herbivore species (e.g., Lawton & Schroder, 1977; Kennedy & Southwood, 1984). How-

ever, these studies did not properly include the full phylogenetic relationships between host-plant species. As species are related to one another in a hierarchical fashion, they therefore cannot be considered as statistically independent units (Martins & Garland, 1991). Later studies involved the use of comparative methods, which allowed the inclusion of the phylogeny of species under analysis, without the confounding effects of the host species phylogenetic relationships (Harvey & Pagel, 1991; Martins & Hansen, 1996). Several methods are available that incorporate phylogenies and account for the historical dependence among taxa, such as the independent contrasts (Felsenstein, 1985) and phylogenetic autocorrelation (Cheverud, Dow, & Leutenegger, 1985) techniques. Thus, Kelly & Southwood, (1999) incorporated phylogenetic relationships among British host trees and found that tree availability (range and abundance) was still a good predictor of insect-species richness. Using a similar approach, Brändle & Brandl, (2001) confirmed that patterns derived from the fauna of the British isles were also valid for continental situations. In both cases, the host plants studied belonged to distant taxa and their phylogenetic relationships did not affect significantly species area as the main explaining factor. However, given that related hosts have chemical and physical traits in common, which might increase an insect’s host range and facilitate host switches (Becerra, 1997; Strong, Lawton, & Southwood, 1984),

phylogenetically close host plants are expected to share more herbivores than unrelated host plants (Novotny et al., 2002), thus increasing the relative importance of phylogenetic affinities among host plants on insect–plant associations. Therefore, in studies of closely related host-plant species, the effect of host phylogeny is likely to be important when analysing the species richness of their associated insect herbivores. To our knowledge, no study has addressed the species richness of phytophagous insects on hosts of the same genus using a phylogenetic approach; furthermore, no such studies have been performed on insect–plant interactions in the Southern hemisphere.

Southern beeches (*Nothofagus*, Nothofagaceae) include 35 taxa distributed in Southern South America, New Zealand, Australia, New Caledonia and New Guinea (Poole, 1987). This disjunct distribution of *Nothofagus* is one of the most studied trans-Antarctic relationships and provides support for the continental drift hypothesis (Hill, 1992). The evolution and phylogenetic history of the genus has been evidenced by its fossil record, biogeography and comparative morphology (Hill, 1992), and a phylogenetic hypothesis has been proposed based on the molecular data (Manos, 1997; Martin & Dowd, 1993). Studies with an emphasis on forestry have yielded an extensive database on insects associated with *Nothofagus* (Carrillo & Cerda, 1987; Gentili & Gentili, 1988; Grandon, 1996). Additional reviews of the insect fauna associated with *Nothofagus* have identified guilds with high levels of diversification and specialisation on different species of *Nothofagus* (McQuillan, 1993). Studies of the biogeographic patterns of *Nothofagus* and some of their associated groups of insect herbivores have provided an understanding of the evolutionary history of insects and their host plants (Humphries, Cox, & Nielsen, 1986; Schlinger, 1974; Starý, 1994). The chemical attributes of *Nothofagus* species did not explain the insect richness (Russell et al., 2000), although in that study other important ecological attributes of *Nothofagus* (such as distribution area, architecture, etc.) were not considered. The present study is aimed at establishing the relative contribution of ecological attributes – including chemical attributes – of *Nothofagus* species to the species richness of their associated insect fauna in South America and New Zealand using a phylogenetic approach.

## Materials and methods

### Databases

The analysis included all *Nothofagus* species described from South America and New Zealand (subgenera according to Manos (1997)). The South American

species were: (Subgenus Fuscospora) *Nothofagus alexandrii* Esp.; (Subgenus Nothofagus) *Nothofagus antarctica* (G. Forster) Oerst., *Nothofagus pumilio* (P. et E.) Krasser, *Nothofagus betuloides* (Mirb.) Oerst., *Nothofagus nitida* (Phil.) Krasser, *Nothofagus dombeyi* (Mirb.) Oerst.; (Subgenus Lophozonia) *Nothofagus alpina* (P. et E.) Oerst., *Nothofagus glauca* (Phil.) Krasser and *Nothofagus obliqua* (Mirb.) Oerst. The New Zealand species were: (Subgenus Fuscospora) *Nothofagus fusca* (Hook. f.) Oerst., *Nothofagus solandri* (Hook. f.) Oerst., *Nothofagus truncata* (Col.) Ckn and (Subgenus Lophozonia) *Nothofagus menziesii* (Hook. f.) Oerst.

### Variables

- (1) *Nothofagus* area of distribution ( $a$ , km<sup>2</sup>), longitudinal (rln) and latitudinal ranges (rlt, degrees). Values were obtained for South America from Gajardo, (1994), which provides distribution maps of different plant associations. All plant associations that included *Nothofagus* species as the main components were included in the analysis. Distribution maps were available for each *Nothofagus* species in the case of New Zealand (Poole, 1987). The maps were scanned and the areas calculated with the software SigmaScan/Image<sup>®</sup> (see Appendix A).
- (2) Architectural complexity ( $c$ ). This parameter was defined by Leather (1986) in terms of the maximum tree height ( $h$ ) and maximum leaf length ( $l$ ) through the equation

$$c = \log(hl^3).$$

The architectural complexity index is biased in favour of the leaf area of the plant, which is more likely to be related to plant complexity for leaf-feeding herbivores (Leather, 1986). The data were obtained from Rodríguez, Matthei, & Quezada (1983) for South America, and from Poole (1987) for New Zealand (see Appendix A).

- (3) *Phytochemical attributes*. These were evaluated from thin-layer chromatographic plates (TLC) of successive dichloromethane and methanol extracts of leaves of all *Nothofagus* species present in South America and New Zealand. Leaves were severed from young branches collected from 4–6 individual trees, mixed, air dried in shade and taken to the laboratory for extraction. Each TLC plate contained spots of the extracts from all species. Four plates were produced for each type of extract. Plates were visualised either with Liebermann reagent, vanillin/sulphuric acid, phosphomolybdic acid or UV light (254 nm), and a list of spots differing in retention factors (i.e. ratio of chromatographic spot migration in relation to solvent migration,  $R_f$ ) was produced for each plate. The data of the presence or absence of each of the chromatographic spots for each

species were used to evaluate chemical diversity and uniqueness, as proposed by Jones & Lawton (1991). Chemical diversity ( $d$ ) was defined as the number of spots detected for each *Nothofagus* species ( $d_{\min} = 19$ ,  $d_{\max} = 48$ , total different spots observed = 123). Chemical uniqueness ( $u$ ) was defined as a measure of particular or unusual chemistry present in a given species in relation to other related species, and was calculated with the equation given by Jones & Lawton (1991) as

$$u = \sum_{i=1}^d P_i/d,$$

where  $P_i$  is the proportion of all *Nothofagus* species containing the compound  $i$  and  $d$  is the chemical diversity already defined above ( $u_{\min} = 0.14$ ,  $u_{\max} = 0.40$ , see Appendix A).

- (4) *Species richness* ( $S$ ). Information on insects associated with *Nothofagus* was obtained from McQuillan (1993), Gentili & Gentili (1988), Grandon (1996) and Fuentes-Contreras, Muñoz, & Niemeyer (1997). The insects were assigned to the following guilds: leaf chewers, sap feeders and wood borers (this includes all borers and miners in shoots, stems, bark, etc.). These guilds were selected because they concentrate the main part of the reported *Nothofagus*–insect associations in the literature cited above. Insects were also taxonomically classified as Coleoptera or Lepidoptera, whereas the sap-feeding guild consisted exclusively of species from the order Hemiptera (see Appendix A).

## Phylogenetic analyses

Phylogenetically independent contrasts were obtained for all log-transformed variables (Felsenstein, 1985). All transformations improved the normality of the data. All subsequent references to these variables refer to the transformed data. The *Nothofagus* phylogeny used was the combined consensus tree, based on combined analysis of rDNA ITS sequences, chloroplast DNA *rbcL* sequences and morphological characters, which offer the best available estimate of the phylogeny of this genus (Manos, 1997). The method of independent contrasts requires a fully resolved tree as well as branch length, and assumes that evolution of the characteristics under study follows a Brownian motion model (Felsenstein, 1985). A punctuated evolutionary model was assumed. For this analysis the initial branch length was set to one. The diagnostic proposed by Garland, Harvey, & Ives (1992) revealed that the contrasts were appropriately standardised. The main reason for standardising contrasts is to obtain equal weighting, allowing the use of probability tables for

statistical tests (Garland et al., 1992). The goal of independent contrasts is thus to transform the original data into independent and equally distributed contrasts. This is similar to standard statistical comparisons and analyses, with the only constraint that all models are forced through the origin, a requirement of the independent contrast algorithm (Garland et al., 1992). The standardised phylogenetic independent contrasts were used in the forward stepwise multiple regression analysis computed through the origin (Garland et al., 1992). Independent contrasts were carried out with the program COMPARE (Martins, 2003), which implements a variety of methods for continuous variables. A non-phylogenetic analysis was performed for comparative purposes, as there are studies that have reached the same conclusions using normal multiple (non-phylogenetic) regression and the independent contrasts method.

Since South America, contrary to New Zealand, has *Nothofagus* species with extensive latitudinal ranges, we explored the possibility that the distribution range of South American species had a major influence on insect species richness by performing a new analysis using phylogenetically independent contrasts obtained for South American species only.

## Results

The results of multiple regressions using a non-phylogenetic analysis and the punctuated evolutionary model are shown in Table 1. When all insect species were included and a non-phylogenetic analysis was performed, area and chemical uniqueness were the most relevant host-plant attributes to explain associated insect richness (Table 1). On the other hand, only latitudinal range was a relevant host-plant attribute using the phylogenetic approach (Fig. 1). The results of independent contrasts for insect guilds and taxonomic orders using the punctuated evolutionary model showed that, with the exception of the sap feeders, three variables were included in the regression equations: latitudinal range and architectural complexity had positive effects, while chemical uniqueness negatively affected insect species richness (Table 1). For sap feeders, longitudinal range, chemical diversity and distribution area entered the regressions when using independent contrasts, as compared to the non-phylogenetic analysis where architectural complexity and latitudinal and longitudinal ranges explained species richness.

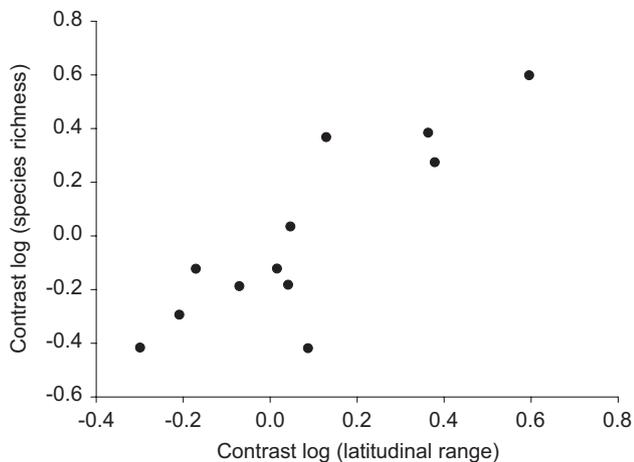
Scatter plots of the untransformed data revealed a negative relationship between species richness and chemical uniqueness of *Nothofagus* species, with *N. glauca* as a clear outlier (Fig. 2): thus, although *N. glauca* had a comparatively common chemistry, it has a low associated insect species richness.

**Table 1.** Stepwise multiple regressions for the insects associated with *Nothofagus* for all insect species, according to guild and taxonomic order

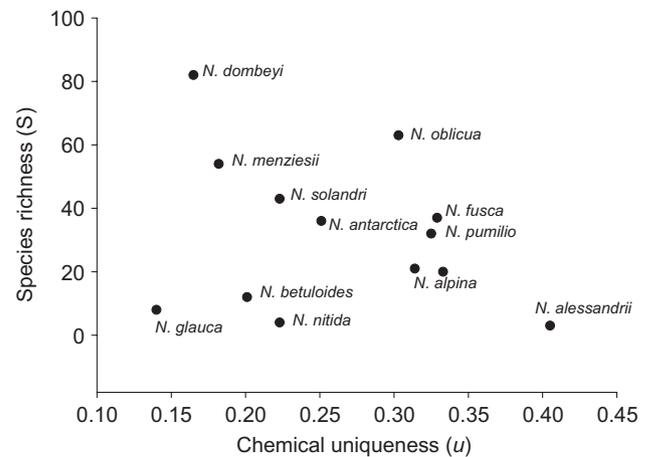
Dependent variable	Regression equation	Multiple $r^2$	d.f.	$F$
<i>All species</i>				
Non-phylogenetic	$S = 0.82a + 0.17u$	0.98	2/10	125.83***
Punctuated	$S = 0.81rlt$	0.66	1/11	21.01**
<i>Chewers</i>				
Non-phylogenetic	$S = 0.93a$	0.93	1/12	81.17***
Punctuated	$S = 1.14rlt + 0.47c - 0.23u$	0.80	3/9	12.08**
<i>Sap-feeders</i>				
Non-phylogenetic	$S = 1.10rln + 0.29c - 0.40rlt$	0.97	3/10	49.55***
Punctuated	$S = 0.94rln + 0.73u + 0.45d - 0.57a$	0.66	4/8	3.86*
<i>Borers</i>				
Non-phylogenetic	$S = 0.91rlt$	0.82	1/12	54.5***
Punctuated	$S = 1.23rlt + 0.80c - 0.64u$	0.74	3/9	8.52**
<i>Coleoptera</i>				
Non-phylogenetic	$S = 0.91rlt$	0.83	1/12	58.7***
Punctuated	$S = 1.22rlt + 0.78c - 0.40u$	0.73	3/9	8.27**
<i>Lepidoptera</i>				
Non-phylogenetic	$S = 0.88rln$	0.78	1/12	41.45***
Punctuated	$S = 1.21rlt + 0.70c - 0.38u$	0.77	3/9	9.77**

The equations represent the non-phylogenetic analysis and analyses obtained with assumptions of punctuated evolution.  $a$  = area,  $c$  = architectural complexity,  $u$  = chemical uniqueness,  $d$  = chemical diversity,  $rlt$  = latitudinal range,  $rln$  = longitudinal range,  $S$  = species richness.

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

**Fig. 1.** Relationship between the contrasts of the  $\log_{10}$ (latitudinal range) and the contrasts of the  $\log_{10}$ (insect-species richness).

The phylogenetic analysis including only values for South American species revealed that the latitudinal range of *Nothofagus* species was the only recurrent variable included in the models (Table 2). For sap feeders, two additional variables, area and chemical uniqueness, were identified, but the regression was not statistically significant (Table 2).

**Fig. 2.** Scatterplots of the relationship of chemical uniqueness and insect-species richness (untransformed data).

## Discussion

The non-phylogenetic analysis (Table 1) indicates that the area of distribution and chemical uniqueness of the *Nothofagus* host has an important influence on the total species richness of the associated insects. Although non-phylogenetic is not recommended, and we have only

**Table 2.** Stepwise multiple regressions for the insects associated with *Nothofagus* species from South America for all insect species, according to guild and taxonomic order

Dependent variable	Regression equation	Multiple $r^2$	d.f.	$F$
All species	$S = 0.83 \text{ rlt}$	0.69	1/7	15.32 **
Chewers	$S = 0.86 \text{ rlt}$	0.74	1/7	20.03 **
Sap feeders	$S = -0.76a - 0.85u + 1.05 \text{ rlt}$	0.56	3/5	2.12 NS
Borers	$S = 0.84 \text{ rlt}$	0.71	1/7	16.84 **
Coleoptera	$S = 0.85 \text{ rlt}$	0.73	1/7	18.55 **
Lepidoptera	$S = 0.86 \text{ rlt}$	0.73	1/7	19.35 **

The equations represent the analysis obtained with assumptions of punctuated evolution.  $a$  = area,  $c$  = architectural complexity,  $u$  = chemical uniqueness, rlt = latitudinal range, rln = longitudinal range,  $S$  = species richness.

$P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , NS,  $P > 0.05$ .

included it here as a comparison, this result is in agreement with the majority of similar analyses performed on insect–plant associations (Basset & Burckhardt, 1992; Cornell, 1985, 1986; Hatcher, 1994; Jones et al., 1991; Lawton & Schroder, 1977, 1979; Leather, 1986). Until now, to our knowledge, a few studies have included plant chemistry as a variable to explain species richness (e.g. Jones & Lawton, 1991). As such, chemical uniqueness partly explains richness when a non-phylogenetic analysis is performed. On the other hand, the analysis by independent contrasts within the *Nothofagus* genus revealed that latitudinal range was an important factor that determines the associated insect richness (Fig. 1). This was true for all guilds and taxonomic orders with the exception of sap feeders (Table 1). Latitudinal and longitudinal ranges have also been highlighted as important factors explaining patterns of species richness of vertebrates (Brown, 1995; Brown & Lomolino, 1998) and insects (Andrew & Hughes, 2005; Blanche & Westoby, 1996). Area of distribution is related to latitudinal and longitudinal ranges, but plant species with similar areas of distribution might have different latitudinal ranges. For instance, our data show that *N. alpina* and *N. glauca* have a similar area of distribution but in *N. alpina* latitudinal distribution is almost four times longer and twice as many herbivores are associated. The same is true for *N. nitida* and *N. antarctica*. Increased latitudinal range of the host plant will be associated with increased numbers of herbivore species (Andrew & Hughes, 2005). It is worth noting that latitudinal range itself is not responsible for increasing species richness and factors such as climate variation, predation and productivity, among others, are the most probable causes (Brown, 1995).

Analyses restricted to South American species indicate that latitudinal range is the key factor to explain the richness of all guilds and taxonomic orders of associated herbivore insects, with the exception of the sap feeders. Unlike the complete analysis, neither architectural complexity nor chemical uniqueness were important to explain associated insect species richness.

The distribution of the flora, including *Nothofagus* in South America, is limited by the orientation of the main geographic barriers, such as mountain chains or main rivers (Arroyo, 1995; Solervicens, 1995). Our data suggest that this is the case of the South American species of *Nothofagus* and their associated insects. Unfortunately, the number of *Nothofagus* species in New Zealand ( $S = 4$ ) is too low to perform a multiple regression which could be reasonably compared with results from South America.

The sap feeders appear to be an ecological guild that is more affected by other ecological features of *Nothofagus* species, which were not included in this analysis. Although different factors entered the equations, they were not significant in explaining species richness (Table 2). Other features that are not directly involved with the host plant could have an important role in explaining the species richness of aphids, such as predator–parasitoid richness or environmental factors directly affecting the herbivores.

Architectural complexity, a factor which commonly influences insect species richness (Lawton et al., 1977), was also positively correlated with insect species richness when using independent contrasts. Given that plants with higher architectural complexity show increased spatial resource distribution and abundance of high-quality sites such as apical meristems, they represent a more heterogeneous habitat which can support higher insect species richness.

The independent contrast analysis shows that species with unique chemical attributes have less associated species. For example, *N. alessandrii*, a species with the most unique chemistry among *Nothofagus*, has very few and mostly specialised herbivores (Fuentes-Contreras et al., 1997; Gaete-Eastman, Figueroa, Olivares-Donoso, Niemeyer, & Ramírez, 2004). Previous studies have highlighted *N. alessandrii* as a species particularly well defended against herbivory. Apparently the metabolites pinosylvin and galangin would be responsible for the antifeedant activity (Russell et al., 2000). Leaf volatiles are also likely to be important in explaining the

aphid host affiliation in this species (Russell, Faúndez, & Niemeyer, 2004). In contrast, *N. dombeyi* with a very common chemistry has the highest number of related insect species. A clear exception is *N. glauca* (see Fig. 2) that does not fit with the negative relation between chemical uniqueness and species richness. Although *N. glauca* has a very common chemistry, it has a low associated insect species richness, but at the same time also has a rather low latitudinal range (Fig. 1). Coincidentally, though, all species related to *N. glauca* are found on the other South American *Nothofagus* (Grandon, 1996; McQuillan, 1993).

The negative association between chemical uniqueness and insect species richness could be related to the fact that the vast majority of phytophagous insects are highly specialised in their feeding habits, so that, among other factors primary plant substances usually restrict host-plant use (Ehrlich & Raven 1964; Fox & Morrow, 1981). Indeed, secondary plant substances strongly constrain phytophagous insects to shift among host plants that are chemically different (Farrell, 1998). There is some molecular phylogenetic evidence to confirm that secondary chemistry could explain host shifts better than plant phylogeny and plant geographic distribution (Becerra, 1997; Futuyma & McCafferty, 1990). Chemical uniqueness may result from “key innovations,” driving herbivore specialisation and therefore reducing the number of species which can use the plant resources (Berenbaum, Favret, & Schuler, 1996). However, there is growing consensus that not only plant chemistry but also a suite of other parameters influence host affiliation (Bernays, 1998; Joshi & Thompson, 1995). Nevertheless, the chemical properties of the host plant are an important factor to explain associated species richness at the community level.

Overall, unlike the work of Kelly & Southwood (1999) for the British Isles and the results found by Brändle & Brandl (2001) for Germany, host-plant attributes explaining insect species richness are affected by the phylogenetic relationships among the tree species involved (Table 1: non-phylogenetic vs. punctuated). In our case, within the genus *Nothofagus*, independent contrasts showed that the most important factor affecting insect species richness is also tree availability (= range and abundance, sensu Kelly & Southwood, 1999), but perhaps latitudinal and longitudinal ranges should also be considered in these types of studies. In addition, chemical uniqueness should limit species resource use by species. Clearly, a suite of parameters, including plant chemistry, will best explain host affiliation.

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## Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.baae.2007.11.009](https://doi.org/10.1016/j.baae.2007.11.009).

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