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RESEARCH ARTICLE

Why so many apparently rare beetles in Chilean temperate rainforests? ¿Por qué hay tantos coleópteros presuntamente raros en los bosques templados de Chile?

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ABSTRACT

Species abundance curves were calculated from data sets collected by fogging 52 trees in *Nothofagus* forest (~46000 specimens) and 24 trees in *Araucaria* forest (~15000 specimens) in Chile. Neither data set fitted the standard species abundance models. Like similar data sets collected from tropical forests, there were too many species represented by single specimens. The proposal that these were vagrants normally found on other tree species was not supported as, unlike tropical forests, *Nothofagus* forests are not diverse, often consisting of single species stands. Examination of three assumptions of the most parsimonious equilibrium models showed them to be false. Between them the observations of undersampling bias, community disequilibria and combining data from different feeding guilds with different species abundance curves are likely to be sufficient to explain the divergence of data for large speciose beetle communities from the predictions of any of the equilibrium models. Until these three factors can be fully accounted for and residual divergence detected, there is no necessity to propose further, more complex, mechanisms to explain such data sets. Estimated values of alpha and Simpson D were shown to be strongly sample size dependent, affecting their value as estimators of biological diversity.

Key words: species abundance curves, biodiversity estimation, body size and density.

RESUMEN

Se calcularon curvas de abundancia de especies a partir de datos obtenidos por medio de nebulización de 52 árboles en bosques de *Nothofagus* (aproximadamente 46000 ejemplares) y 24 árboles en bosques de *Araucaria araucana* (aproximadamente 15000 ejemplares) en Chile. Los datos obtenidos no se ajustan a los modelos estándares de abundancia de especies, al igual que los datos obtenidos de bosques tropicales, existen muchas especies representadas por ejemplares únicos.

La hipótesis de que los mencionados ejemplares únicos son erráticos y que se encuentran normalmente en otros árboles no fue aceptada, contrario a los bosques tropicales, los bosques de *Nothofagus* no son diversos y generalmente lo conforman una sola especie. El análisis de tres supuestos a partir de los modelos de equilibrio más parsimoniosos, demostró que dichos modelos son falsos. Entre ellos, las observaciones de muestreo afectadas por sesgo, desequilibrio de la comunidad y la combinación de datos procedentes de distintos estratos alimenticios con diferentes curvas de abundancia de especies, parecen ser suficientes para poder explicar la divergencia de los datos para las comunidades de coleópteros con alto número de especies, a partir del supuesto de cualquier modelo de equilibrio. Hasta que estos tres factores se puedan tomar en cuenta y se pueda detectar divergencia residual, no existe necesidad de proponer mecanismos más complejos para explicar dichos datos. Los valores estimados de alfa y Simson D están estrechamente correlacionados al tamaño de la muestra, lo cual afecta su valor como estimador de la diversidad biológica.

Palabras clave: curvas de abundancia de especies, estimadores de diversidad biológica, tamaño corporal y densidad.

INTRODUCTION

There is a need to develop and test the simplest possible models in ecology using the most parsimonious set of assumptions before adding further variables leading to more complex explanations of data sets (e.g., Gotelli & Graves 1996, Hubbell 2001, Magurran

2005, Coddington et al. 2009). The need for such an approach is evident when exploring the assembly rules predicting the relative abundances of species in a community. In some cases one or more of the available models (e.g., Hubbell 2001, Magurran 2004) has been found to fit the patterns seen in field data sets. (e.g., Volkov et al. 2003, Chave 2004, Wootton

2005). Some data sets, however, do not fit any of the models, with tropical rainforest beetle communities providing a notable example (e.g., Morse et al. 1988, Hubbell 2001). Such communities typically have a few species that are more common than any of the models predict and a very large number of rare species. The failure of any of the proposed simple models to fit the observed distribution highlights the limitations of our present understanding of community ecology and has led to more complex suggestions as to reasons for such mismatches (Sugihara 1980, Tokeshi 1996, Harte et al. 1999, Hubbell 2001, Magurran & Henderson 2003) rather than a more critical examination of the assumptions underlying the present models or the nature of the data sets used.

The issue of excessive numbers of species represented by single specimens in samples (singletons) has been addressed by exploring the null hypothesis that the failure of such data sets to fit any of the standard models is due to bias introduced by undersampling (McGill 2003, Coddington et al. 2009). They also noted that intensity (average number of individuals per species in a sample) is commonly very low in arthropod studies (4-70 in beetle studies; Coddington et al. 2009). For their study of a tropical spider community, they estimated that a sampling intensity of 340 was needed to approach an adequate sample for estimating the shape of the species abundance curve in a local community. Further, non-parametric estimators of species numbers (ACE, ICE, Chao 1; defined in Magurran 2004) give serious underestimates of the real number when there is undersampling and that about three quarters of the species in the community need to be sampled before the confidence interval of the estimator includes the true number of species (Walther & Morand 1998). As a consequence, if the sample size is too small then the estimates of the number of species made using ACE, ICE or Chao 1 will vary with sample size, instead on being independent of sample size.

A second possible explanation of the anomalous shape of the species abundance curve for tropical beetles would question the validity of the assumption of most models that the communities are in equilibrium. Communities in early successional stages or in some cases, stressed, have curves similar

to those found for tropical beetle communities (a few very common species and a long tail of rare species e.g., Gray 1979, Kaiser et al. 2000). Possible causes of disequilibria in local communities include them being fugitive communities (with constantly changing membership (Azarbayjani et al. 1999) resulting, for example, from common species being overwhelmed by predators or parasitoids); having clumped distributions (due, for example, to the breeding structure of insect populations or the patchy distribution of resources (Longino et al. 2002)); being subjected to changing environmental conditions (for example, the effects of ecological differences between climatic conditions in different years (e.g., Azarbayjani et al. 1999); being subjected to edge effects (Ewers & Didham 2008); or having insufficient time since establishment to have reached equilibrium (Hurtt & Pacala 1995). Whatever the reason, the assumption that the observed species abundance curves reflect stable communities in equilibrium needs to be questioned.

The unified neutral theory and community apportionment models assume that all species in a modelled community belong to the same trophic level. A third possible explanation then of the divergence of the abundance distribution in field data from predictions challenges the assumption that all species in the community considered belong to the same trophic level and that consequently the observed curve is that of a single community rather than the sum of a series of independent, and different, species abundance curves (Hubbell 2001).

The usual, more complex, explanation of anomalous tropical beetle data is based on the observation that tropical forests contain a very diverse array of tree species. Stork (1997) proposed that the misfit of his data to models is due to the presence on a tree, at low frequency, of transient specimens of beetle species normally found on other host plant species in the highly diverse flora of tropical forest (see also Novotny & Basset 2000, Longino et al. 2002, Magurran & Henderson 2003).

Most studies of the community structure of highly diverse faunas are of tropical arthropod faunas, commonly beetle faunas. Our knowledge of community structures of

temperate faunas is fragmentary (Hammond et al. 1997, Arias et al. 2008, Sobek et al. 2009). As a consequence, the analysis of a temperate beetle fauna data set collected in a similar way to earlier tropical data sets would be of interest.

This paper describes relevant attributes of such a data set which consists of the relative abundances of 938 beetle species collected by fogging 76 trees in the temperate rain forests of Chile. It explores possible explanations of community structure, by testing the three assumptions described above of the most parsimonious models and also examines the more complex explanation offered of the previously observed lack of fit of tropical rainforest beetle communities to predictions.

Assumption 1: If samples of the Chilean beetle community include a large number of rare species, this is due to undersampling

The intensity of sampling will be relatively low. As well, less than three quarters of the predicted species will have been collected and estimates of species numbers obtained using standard estimators (ACE, ICE, MMM, Chao 1; Colwell 2005) will increase with increasing intensity/sample size instead of being independent of sample size.

Assumption 2: If samples of the Chilean beetle community include a large number of rare species, this is due to community disequilibria

The relatively recent re-establishment of the Chilean forests of the Andean foothills after the last glacial period (14 000 years BP), unlike the long-established coastal forests, offers one possible opportunity to detect a disequilibrium (Ashworth & Hoganson 1993). If recovery to equilibrium is slow (Harte et al. 1999), we would expect the Andean foothill metapopulations to be less diverse and further from equilibrium than those in coastal forests that were not wiped out by glaciation.

If disequilibrium is due to the ephemeral clustering of sets of species at a particular time and location, then sampling the same location on occasions separated by several years should give a pattern where samples from the same year are more similar than samples from different years.

Assumption 3: If samples of the Chilean beetle community include a large number of rare species, this is due to species belonging to different trophic levels being treated as a single 'community'

The unified neutral theory and community apportionment models assume that all species in the community considered belong to the same trophic level. In fact, the beetles collected in the present study belong to a range of different feeding guilds and it is known that the community structures of these guilds differ (Arias et al. 2008). If the analyses described above are repeated with beetles from different feeding guilds considered separately then the apparent excess of singletons should disappear.

The presence of excessive numbers of rare beetle species in tropical forests is due to the presence of vagrants coming from other species of host trees

The structure of the temperate Chilean forests is different to that found in tropical rainforests, with only a relatively low diversity of host plants present in an area (McQuillan 1993). If Stork's explanation, that the large number of singletons in the tropical beetle community he studied is due to vagrant specimens of species living on other tree species, is true (Stork 1997), the limited number of tree species in Chilean temperate forests would result in a much smaller pool of vagrants and the beetle community would not include the large number of rare species seen in samples from tropical forests.

Singletons, on average, will have a larger body size than more common species

As well as the issue of the adequacy of the assumptions of the simpler theories, the data set offers the opportunity to explore another matter related to relative species abundance. Coddington et al. (2009) observed that the average size of species represented by singletons in their spider study was larger than that of all species sampled. This result is consistent with observations made on many groups (e.g., Lawton 1990).

METHODS

The community structures of the coleopteran faunas found on separate trees in Chilean *Araucaria* and *Nothofagus* forests has been analysed by Arias et al. (2008). The material was collected by canopy fogging and they provide details of the collecting, sorting and identification methods used. In the present study, the sample set of 29 trees analysed in Arias et al. (2008) was increased to include material from 24 *Araucaria* (*Araucaria araucana* (Molina)) trees and 52 *Nothofagus* trees through the addition of data from more years.. The material was collected over summer in six years between 2001 and 2008 and was taken from forests in both the Andean foothills and the coastal ranges between the latitudes of 37° and 42° S in Chile. The *Nothofagus* trees were of a combined data set from the very similar *Nothofagus dombeyi* (Mirb.) Blume, *N. obliqua* (Birb.) Blume, and *N. nitida* (Phil.) Krasser. Cluster analysis of the Jacquard Indices for these faunas showed the faunas of the different *Nothofagus* tree species were interspersed and there was no evidence that required them to be analysed separately in this analysis (Arias et al. (2008) and unpublished data).

Estimates of richness and diversity as number of individuals (N), observed number of species (S_{obs}), predicted number of species (ACE, ICE, MMM, Chao 1), intensity (N/S_{obs}), alpha and Simpson D were calculated using Estimate S (Colwell 2005). An estimate of the observed shape of the metacommunity curve was obtained by combining all the field samples (Hubbell 2001). Values for the fundamental biodiversity number (θ , Hubbell 2001) and the migration rate (m) from the metacommunity into local communities were calculated from this curve using maximum likelihood methods (TeTame, Chave & Jabot 2006). The predicted shape of the logseries and truncated lognormal curves were calculated following Magurran (2004) and the shape predicted by neutral theory following Hubbell & Borda de Agua (2004). Gotelli & Colwell (2001) highlight the issue of comparing estimates developed using unequal number of individuals and data is presented for approximately equal numbers of individuals when relevant.

The size (as volume) of specimens of each species was estimated by multiplying the median length, height and width of up to (and preferably) three specimens of a species. Not all species however were measured.

RESULTS

Summaries of the basic parameters of the *Nothofagus* and *Araucaria* beetle communities studied are given in Table 1 and Fig. 1. The general attributes of the communities in the two forest types are consistent with those reported by Arias et al. (2008). The observed and predicted number of species found in the *Nothofagus* forest are much higher than those found in the *Araucaria* forest. The species accumulation curves are not approaching asymptotes (Fig. 1).

If samples of the Chilean beetle community include a large number of rare species, this is due to undersampling

Arias et al. (2008) questioned the adequacy of the predictions of total species diversity they obtained because of the variation in the predictions with sample size. With the addition of data from more samples, the predicted number of species on *Araucaria* for example has changed from the 168 observed and 211 predicted (Chao 1) species on ten trees in Arias et al. (2008) to 296 observed and 373 predicted on 24 trees. Examination of Fig. 1 shows that, even with the larger sample sizes, none of the predictors of the number of species have stabilised, and they continue to rise with increasing sample size. While the proportion of species predicted that were actually sampled is estimated to be approximately 80 % (Table 1) and, therefore above the minimum recommended level allowing the use of the estimators (Walther & Morand 1998), the predictions have not stabilised. The absolute number of singletons rises until the 49th tree and then begins to drop in the *Nothofagus* forest, though the number of doubletons continues to increase. In the *Araucaria* forest the numbers continue to rise through the 24 trees sampled. The number of doubletons steadily increases with sample size in both cases. The intensity of sampling (55 and 54; Table 1) is in the high range for published studies (4-70) but below that suggested by Coddington et al. (2009; 340+) for a tropical spider community to avoid undersampling.

If samples of the Chilean beetle community include a large number of rare species, this is due to community disequilibrium

The shapes of the observed curves and the fitted logseries and truncated log normal models are shown in Fig. 2. It can be seen that for neither forest type do the predicted curves fit the field data; there are always too many singletons (fit to logseries, adjacent cells below five combined; *Nothofagus* forest [$X^2_9 = 84.2$ $P = 0.025$] and *Araucaria* forest [$X^2_{10} = 105.7$ $P < 0.001$]). The observed curve is not intermediate between the logseries and lognormal curves, as is commonly observed, but more extreme. Consequently, the fit of the field data to the

lognormal curve is much worse than that to the logseries prediction. The richness and diversity values (S_{obs} , alpha, θ and Simpson D) for the *Araucaria* community are much lower than those found for the *Nothofagus* community even when adjusted to the same number of trees (Table 1) and continue to rise as the number of samples increases. The estimates of migration rates from the metacommunities into local communities under neutral assumptions are similar.

The diversities found in coastal versus Andean foothill forests are shown in Table 2. The level of diversity in *Nothofagus* forests as observed species, predicted species, alpha, Simpson D and species per tree are all higher in the coastal forest. Given that the estimates are not independent of sample size (Fig. 1) the data for the larger sample in each case was re-analysed to show the average values (over fifty runs) for an approximately equal number of individuals to the smaller sample. The patterns

TABLE 1

Summary of the results for beetle communities in *Nothofagus* and *Araucaria* forests in Chile.

Resumen de los resultados de comunidades de coleópteros en bosques de *Nothofagus* y *Araucarias* en Chile.

	<i>Nothofagus</i> forest	<i>Araucaria</i> forest
No. trees sampled	52	24
No. individuals (combined samples)	46 595	15 883
No. species (combined samples)	846	296
Observed specimens per sample (mean/tree)	896	662
Observed species per sample (mean/tree)	70	39
Observed species (for ~16 000 specimens)	543	296
Intensity (abundance/species)	55.1	53.7
% of species sampled ($S_{\text{obs}}/\text{Chao1}$)	84	79
Predicted no. species (ICE)	1108	622
Predicted no. species (ACE)	998	402
Predicted no. species (MMM)	1058	398
Predicted no. species (Jack1 \pm SD)	1120 \pm 27	452 \pm 19
Predicted no. species (Chao1 \pm SD)	1007 \pm 27	373 \pm 19
Predicted no. species (Hubbell metacommunity)	2122	662
No. singletons (% of total)	21%	30%
No. singletons (0.5-1.5 individuals in Hubbell metacommunity, % of total)	18.5%	10.1%
θ (for metacommunity)	146.97	51.53
Migration rate (m)	0.00317	0.00323
Simpson D (for ~16 000 specimens)	33.5	24.5
Alpha (for ~16 000 specimens)	109.9	51.6

of results were unchanged. For the *Araucaria* forests, observed species, alpha, Simpson D and species per tree are all higher in the coastal forest, however the predicted number of species varies radically between estimators.

Examination of samples taken from the same location in the same or different years shows incomplete clustering within years (Arias et al. 2008). For the largest data set from a single location, taken at Malacahuello on *Araucaria* in four separate years (Fig. 3), it can be seen that the only significant clustering present is within years. There is no evidence

of the maintenance of patterns of diversity in a local community between years.

Community structure will differ with trophic level

Data sets developed by subdividing the fauna into feeding guilds (Arias et al. 2008) were analysed (Table 3; Fig. 4). It can be seen that there are significant differences between the community parameters of the different guilds but little consistency between the patterns seen in *Araucaria* and *Nothofagus* forests. The presence of higher diversity in

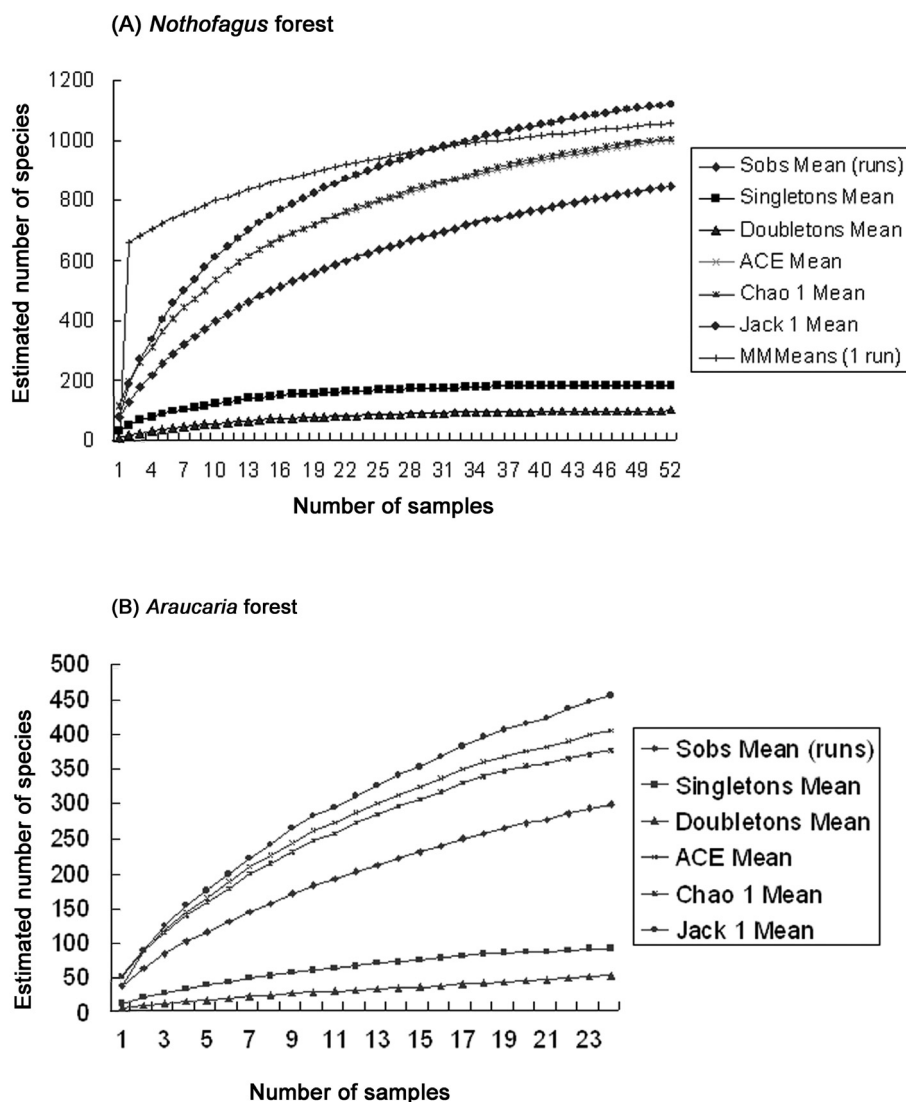


Fig. 1: Accumulation curves over samples sets for beetles collected in: (A) *Nothofagus* forest, (B) *Araucaria* forest.

Curvas de acumulación de muestras de coleópteros colectados en: (A) bosques de *Nothofagus*, (B) bosques de *Araucaria*.

the *Nothofagus* community than the *Araucaria* community is found in all guilds. Comparison of the *Nothofagus* data with the predictions from the fitted logseries curve showed that, when analysed in the Pearson classes 1, 2 and 3+ by Chi squared tests (that is, testing for an excess of singletons and doubletons), there were no significant divergences from predicted for any of the feeding guilds, that is, there is not a significant excess of singletons in the sample. However the combined data was highly divergent ($P < 0.0001$; Fig. 2) when analysed in the same way. The data set for *Araucaria* forest was insufficient to allow an equivalent analysis.

The presence of excessive numbers of rare beetle species in tropical forests is due to the presence of vagrants coming from other species of host trees

Comparison of the temperate rain forest data with a set of tropical rainforest data

(Stork 1997) (Table 2; Fig. 4) shows that the species abundance curves have generally similar forms with several very common species and long tails of singletons. However the number of tropical trees analysed is much fewer and the intensity of sampling is much lower while the predicted number of species and the number of singletons is much greater. A plot of log % singletons against log intensity (Fig. 5) shows that the point for the tropical rainforest beetle data lies just below the regression line for the *Nothofagus* data. If a *Nothofagus* forest was sampled with an intensity similar to that of the Borneo study, (intensity of 5 rather than 42) then an estimated 60 % rather than 58 % singletons found in the Borneo forest would have been observed. This is contrary to the prediction that many more singletons would be expected in a tropical forest sample than in a temperate one with little floral diversity.

TABLE 2

A comparison of the community structures of Borneo, Andean and coastal forests. 'total:' values for all trees combined, 'matching:' mean values for a subset of trees providing a sample of approximately equivalent number of individuals to that in the other area (sampling bootstrapped 50 times). *These numbers are identical entirely by chance.

Comparación de las comunidades de Borneo, cordillera de la Costa y cordillera de los Andes. 'total': valores para todos los árboles combinados, 'correspondencia' de valores promedios para submuestras de árboles equivalente al número de árboles en la otra área muestreada (muestreada 50 veces).

	<i>Nothofagus</i> forest						
	Borneo (Stork, 1997)	Coastal (total)	Coastal (matching)	Andean	Coastal (total)	Andean (matching)	Andean
Specimens per tree	392	920		866	819		567
Species per tree		85.0		53.4	53.2		31.2
No. trees	10	29	22	23	9	13	15
Total specimens	3924	26669	20232	19926	7374*	7374*	8509
Total species	861	642	579	463	196	164	179
Intensity	4.6	42		43	38		48
Estimated species (ACE)		763	707	620	259	235	251
Estimated species (ICE)		876	853	749	381	414	455
Estimated species Chao 1 \pm SD	1781	779 \pm 26	720 \pm 27	610 \pm 28	237 \pm 13	228 \pm 19	241 \pm 19
Alpha (\pm SD)	341	118 \pm 2	112 \pm 2	85 \pm 2	37 \pm 1	24 \pm 1	32 \pm 1
Simpson D \pm SD	70	30 \pm 5	30	22	20	18 \pm 2	18

Singletons have, on average, a larger body size

Mean size (volume \pm SE (n)) of the singleton species measured is 174.3 ± 51.6 (39), of species represented by 2-5 specimens is 72.1 ± 23.0 (83) and for > 5 specimens is 34.7 ± 14.0 (307). Singletons are clearly, on average, larger than more common species.

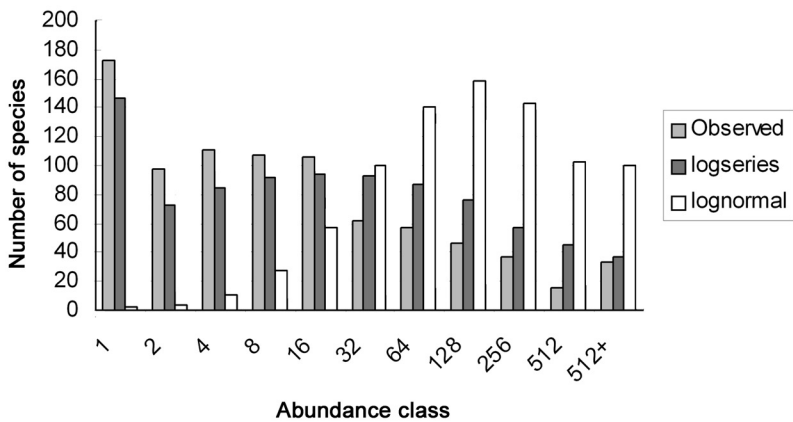
DISCUSSION

The beetle diversity in *Nothofagus* forest is much higher than that in *Araucaria* forest,

whether measured as observed number of species, alpha, θ or Simpson D (Table 1). The intensity (specimens per species) is similar in the two forests as is the estimated migration rates from metacommunities to local communities. On single trees, the number of species and specimens are much lower on *Araucaria* than *Nothofagus*. There is little doubt that the communities in the two forest types are significantly different.

It is possible that the different distributions are due to different attributes of the underlying trees communities. However, both *Nothofagus dombeyi* and

(A) *Nothofagus* forest



(B) *Araucaria* forest

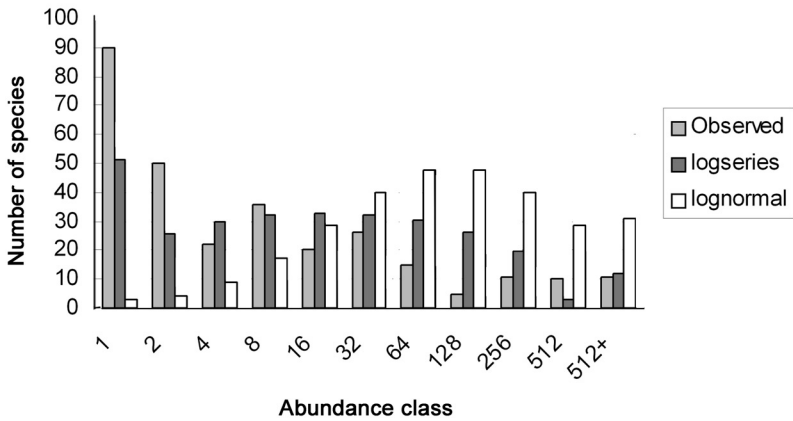


Fig. 2: Fit of observed beetle community data from to local community species abundance curves developed by modelling using the predicted logseries curve.

Ajuste observado de los datos de la comunidad local de coleópteros a una curva acumulada de abundancia de especies desarrolladas a partir de modelos usando la curva de logseries pronosticada.

Araucaria araucana have comparatively high levels of allozyme polymorphism ($H_T = 0.228$ and 0.212 respectively) and geographically structured populations ($H_S = 0.199$ and 0.151 respectively) (Premoli 1997, Premoli & Kitzberger 2005, Ruiz et al. 2007). Consequently, the different community structuring observed in the beetle communities is not simply due to underlying differences in genetic diversity or the level of geographical structuring of the 'host' tree populations. It is possible that the differences are related to the fact that there are different densities of trees in the two forest types. As tree densities are estimated to be 25 trees per hectare in *Araucaria* forest (Smith et al. 2009) and 250 trees per hectare in *Nothofagus* forest (McQuillan 1993), less beetle species would be predicted on *Araucaria* (Hubbell 2004).

The percentage of species collected (S_{obs}/S_{pred}) should have been large enough to allow

the standard predictors to be used (Walther & Morand 1998). However, the estimations have not stabilised. The different estimators give different values for the predicted number of species, with the Hubbell estimate (Table 1) being much higher than the other estimators. It might be possible to use the estimates as the lower bound of the number of species likely to be present; however this can be very misleading. Arias et al. (2007), using the Chao 1 estimator and 12 348 specimens, give the estimated number of species in the *Nothofagus* forest to be 407 (362-481), while the extended study presented here gives 1007 (962-1070).

Commonly used surrogates of biological diversity (alpha, Simpson D) are also strongly affected by sample size, for example, alpha for the *Nothofagus* beetle community varies from 21 for a single tree sample, 60 for five trees combined, to 146 for 52 trees. Such sample size dependence makes them useless as estimators of biological diversity.

Assumptions of the more parsimonious models of community structure described above, as well as the more complex explanation offered of the previously observed lack of fit of tropical rainforest beetle communities to predictions, can now be explored.

If samples of the Chilean beetle community include a large number of rare species, this is due to undersampling

The prediction that standard estimators would increase with increasing sample size is confirmed (Fig. 1) even though the proportion sampled has reached approximately 80 % (Table 1) of the predicted number of species (Fig. 1) and the estimations should have stabilised. The intensity of sampling, about 55, is comparable to values in other large studies (listed in Coddington et al. 2009). The number of singletons rises until the 49th tree and then begins to drop in the *Nothofagus* forest, though the number of doubletons continues to increase. In the *Araucaria* forest the numbers continues to rise through the 24 trees sampled. It is clear that even with collections from 52 trees, undersampling is a significant problem and contributes to the large number of singletons observed.

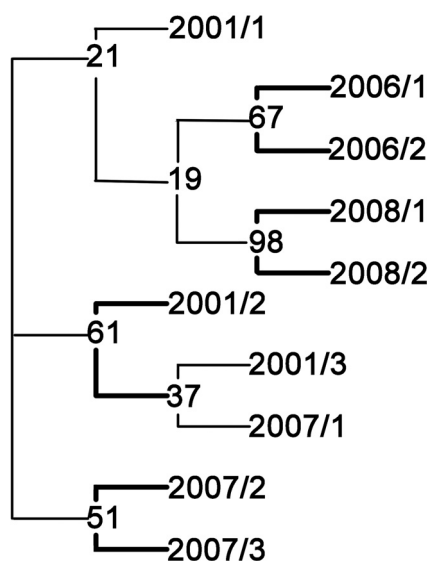


Fig. 3: Relationships between samples collected at a single location in four years. The Distance/Similarity measure is Canberra Distance linked using Saitou and Nei Neighbour Joining (year/sample number shown). The broader lines identify linkages of > 50 %.

Relación entre las muestras colectadas en una localidad específica durante 4 años. La medida de Distancia/Similitud es una distancia Canberra con el uso de Saitou and Nei Neighbour Joining. Las líneas más anchas identifican las conexiones de > 50 %.

If samples of the Chilean beetle community include a large number of rare species, this is due to community disequilibria

The re-establishment of the forests of the Andean foothills after the last glacial period provides an opportunity to detect long term disequilibria. If so, we would expect the Andean foothill metapopulations to be less diverse and further from equilibrium than those in coastal forests that were not wiped out by glaciation. Table 2 shows comparisons of Andean and coastal forest faunas. It is clear that, especially

in *Nothofagus* forests, Andean diversity is lower than coastal diversity after 14000 years. Hurtt & Pacala (1995) showed that communities could remain in disequilibrium indefinitely when dispersal and recruitment are limited. In the present case the immigration of species from the metapopulation into a local population was estimated, under neutral theory, to be 0.003 per generation for both forest types.

If disequilibrium is due to clustering of sets of species at a particular location in a particular year, then sampling the same location in the same or different years should

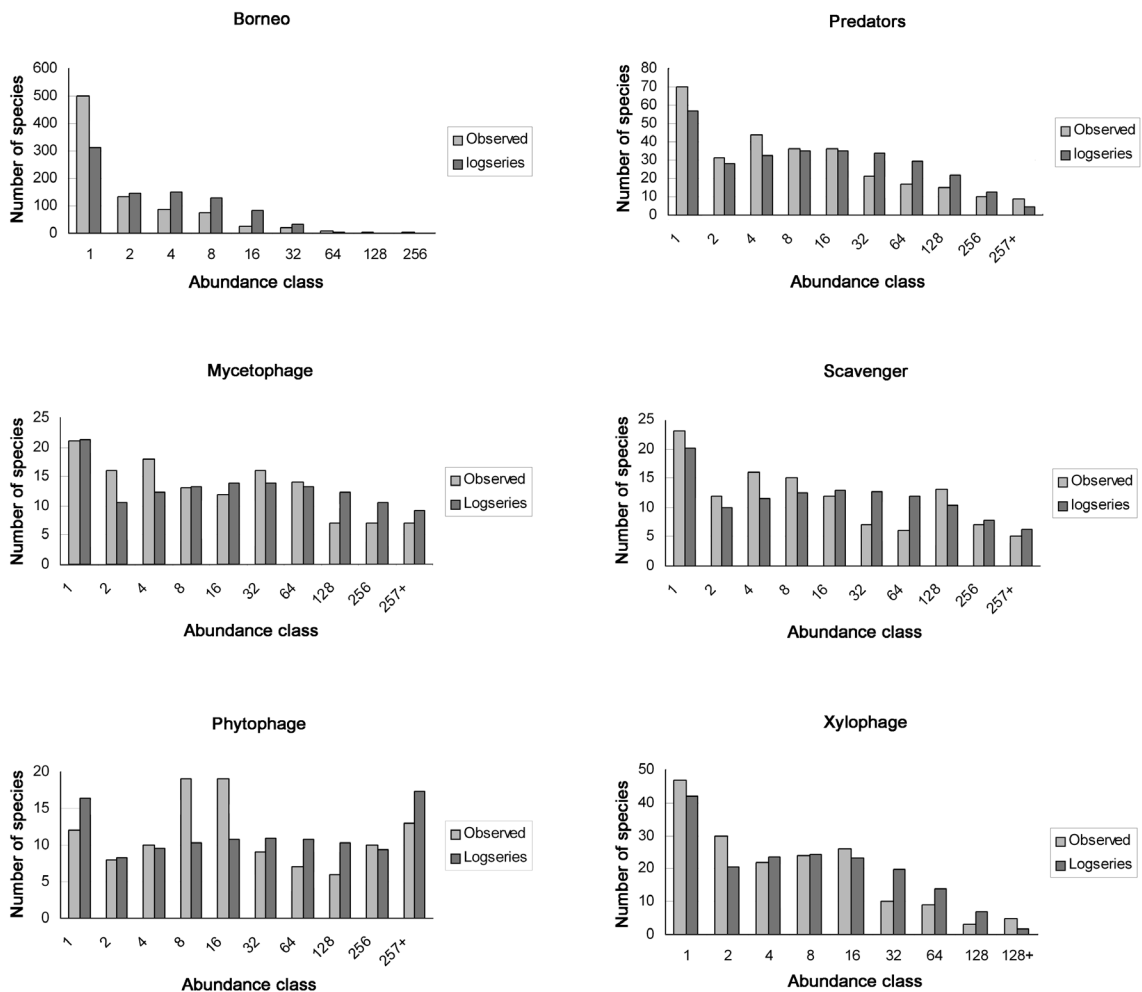


Fig. 4: Fit of observed beetle community data for data for Borneo beetles from Stork (1997) and each trophic group from *Nothofagus* forest to species abundance curves developed by modelling using the predicted logseries curve.

Ajuste de los datos observados de la comunidad local de coleópteros (extraído de Stork 1997) y cada grupo trófico de los bosques de *Nothofagus* a las curva de abundancia de especies desarrolladas a partir de los modelos usando la curva logseries pronosticada.

show clustering of samples within years. Fig. 3 shows such a pattern, with the species from samples taken in the *Araucaria* forest at a single location near Malalcahuello on *Araucaria* in four separate years, being more similar within years than between years. The type III survivorship curve typical of insects (i.e. large numbers of offspring with low average survival rates, compared to the type I pattern of few offspring and relatively high survival rates seen in terrestrial vertebrates) and a non-normal distribution of surviving offspring between parents would further exacerbate the temporal clustering effect and divergence from equilibrium in the direction observed. This is especially an issue when data sets are collected as a series of samples (here a set of specimens from a tree) rather than as independent individuals (Gotelli & Coddington 2001).

It is clear that there is evidence of disequilibria present in the data set. There could well be other factors also causing disequilibria. Whatever the causes, however, the assumptions of the models are not met.

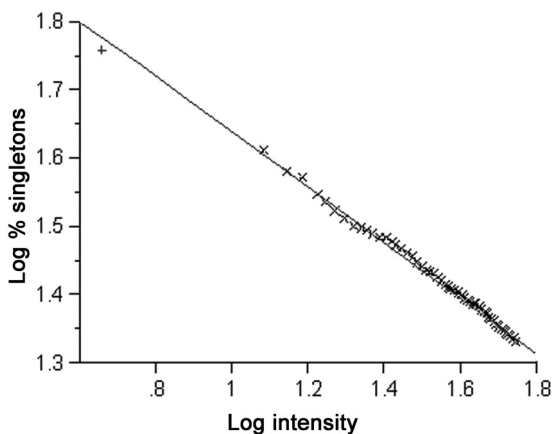


Fig. 5: Regression plot of log % singletons against log intensity for *Nothofagus* forest samples (X). Also shown is the point for the tropical rainforest beetle data of Stork (1997) (+) which lies below the regression line for the *Nothofagus* data, not far above the line as predicted.

Plot de regresión del log % singleton comparado con el log de intensidad para muestras de bosques de *Nothofagus* (X). Se muestra el punto para los coleópteros de comunidades tropicales (Stork 1997) (+) el cual está por debajo de la curva de regresión de la línea de los datos de *Nothofagus*, no muy lejos de la línea pronosticada.

Community structure will differ with trophic level

The unified neutral theory and community apportionment models assume that all species in the community considered belong to the same trophic level, that is, compete for the same resources (Hubbell 2001). When the analyses are repeated with beetles from different feeding guilds considered separately, the higher overall biodiversity observed in *Nothofagus* forest relative to *Araucaria* forest is found consistently in all trophic groups (Table 3). The relative level of diversity between trophic groups differs markedly in the two forest types and shows no consistent pattern other than the predators being the most diverse group in both cases. The null hypothesis of a single community with a single set of diversity parameters is not supported. Tests of the data for each feeding guild separately shows that there is no significant divergence from expected for the singleton and doubleton classes in any case, unlike the combined data set. The abnormal statistics for the overall beetle community is at least in part due to the combination of a series of data sets with markedly different ecological characteristics.

The presence of excessive numbers of rare beetle species in tropical forests is due to the presence of vagrants coming from other species of host trees

The parameters for Borneo rainforest beetles are summarised in Table 2 and Fig. 3. It can be seen that there are more observed and predicted species even with a much smaller sample size. It is also clear that a much higher proportion of singletons were collected. However Coddington et al. (2009) have pointed out that proportionately more singletons will be collected, the lower the intensity of sampling (here, 5 in the Borneo sample; 55 in the Chilean samples) If the value for the Borneo data is plotted on the regression of sampling intensity against the number of singletons for the *Nothofagus* data, to correct for the different intensities (Fig. 5), it is apparent that relatively fewer rather than the predicted more singletons were collected in Borneo. Thus there is no evidence in our comparison to support the hypothesis that tropical rainforest communities contain more singletons than temperate rainforest communities, even though the plant

diversity of tropical forest is much higher than that of Chilean temperate rainforest communities where *Nothofagus* is often found in single species stands. Consequently there is no support for the proposal that the very large number of singletons observed in rainforest beetle communities are primarily due to vagrants from other hosts.

Singletons have, on average, a larger body size

Coddington et al. (2009) observed that the average size of species represented by singletons in their spider study was larger than that of all species sampled but that this effect was due to a few very large cursorial species. A similar result was found in this study with singletons being on average more than five times the size of more common species. This raises another possible source of divergence

from the assumption that the beetle fauna is acting as a single integrated community.

In summary, between them the three null hypotheses of undersampling bias, community disequilibria and feeding guilds with different patterns of diversity are likely to be sufficient to explain the divergence of data for large speciose beetle communities from the predictions of any of the equilibrium models. Until these three factors can be fully accounted for and residual divergence detected, there is no necessity to propose more complex mechanisms to explain such data.

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TABLE 3

Summary of the results for beetle communities in *Nothofagus* and *Araucaria* forests in Chile subdivided into separate feeding guilds.

Resumen de los resultados de comunidades de coleópteros en bosques de *Nothofagus* y *Araucarias* en Chile, subdivididos en estratos alimenticios.

	Individuals	S _{obs}	Intensity	% singletons	ICE	Chao 1 (± SD)	Alpha (± SD)	Simpson
<i>Nothofagus</i> (52 trees):								
Mycetophage	11571	134	86	16	162	146 ± 7	21 ± 1	7
Phytophage	16842	114	148	11	128	121 ± 5	16 ± 1	9
Predator	8833	289	31	24	391	362 ± 20	57 ± 2	29
Scavenger	6435	116	55	20	161	135 ± 9	20 ± 1	13
Xylophage	2603	176	15	27	244	210 ± 12	43 ± 2	21
<i>Nothofagus</i> (similar number of individuals):								
Mycetophage	2670	77	35	25	128	96 ± 10	15 ± 1	7
Phytophage	2591	56	46	23	108	70 ± 8	11 ± 1	77
Predator	2717	168	16	32	342	229 ± 18	40 ± 2	23
Scavenger	2598	78	33	25	140	99 ± 10	15 ± 1	12
Xylophage	2603	176	15	27	244	211 ± 12	43 ± 2	21
<i>Araucaria</i> (24 trees):								
Mycetophage	288	29	10	31	77	34 ± 4	8 ± 1	12
Phytophage	6074	59	103	14	96	61 ± 2	9 ± 1	12
Predator	3801	110	35	35	212	145 ± 13	21 ± 1	6
Scavenger	508	49	10	33	106	60 ± 7	13 ± 1	9
Xylophage	5107	41	125	37	104	76 ± 29	6 ± 1	6

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