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Latitudinal decrease in folivory within *Nothofagus pumilio* forests: dual effect of climate on insect density and leaf traits?

Lucas A. Garibaldi^{1,2*}, Thomas Kitzberger¹ and Adriana Ruggiero¹

¹Laboratorio Ecotono, INIBIOMA-CONICET and Centro Regional Universitario Bariloche-Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina, ²Departamento de Métodos Cuantitativos Aplicados y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Avenue San Martín 4453, C1417DSE Buenos Aires, Argentina

ABSTRACT

Aim The strength of consumer–plant interactions may decrease with latitude. Our objectives were to assess the spatial variation in folivory on *Nothofagus pumilio* and understand the influence of climate on folivory patterns as mediated by changes in folivore density and leaf traits.

Location *Nothofagus pumilio* forests, between 38 and 55°S (Argentina).

Methods We studied the correlation of leaf damage with latitude on data from 47 sampling sites, and evaluated spatial patterns of autocorrelation on latitudinally detrended data with a principal coordinates of neighbour matrices method. Path analysis was used to test the association of temperature and precipitation with leaf damage, mediated by folivore density and leaf traits. We evaluated the adequacy of this ecological model by examining the spatial pattern of autocorrelation in the residuals, and combined spatial and environmental predictors of leaf damage into partial regression.

Results Leaf damage decreased with latitude, which was the only significant spatial predictor. The latitudinal decrease in temperature and precipitation was correlated with a decrease in the density of folivores and leaf size, and diminished leaf damage. Our ecological model adequately explained the spatial autocorrelation in the data: 44% of the variation in leaf damage was explained by the latitudinally structured component of the environment, whereas local environmental effects accounted for another 22%.

Main conclusions We conclude that *N. pumilio* forests show consistent latitudinal patterns of variation in folivory, folivore density and leaf traits. Our study suggests that the latitudinal variation in folivory rates is partly driven by the influence of climate on both plants and herbivores. This warns us about the potential susceptibility of folivory rates to climate warming. We emphasize the value of large-scale analyses as complementary to local experimental approaches to understanding the regulation of herbivory.

Keywords

Herbivory, *Nothofagus pumilio*, partial regression, Patagonia, path analysis, plant–insect interactions, spatial autocorrelation, subantarctic forests.

*Correspondence: Lucas A. Garibaldi, Laboratorio Ecotono, INIBIOMA-CONICET and Centro Regional Universitario Bariloche-Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina.
E-mail: garibald@agro.uba.ar

INTRODUCTION

Latitudinal gradients offer natural scenarios over which to gain understanding of the role of environment in moulding the spatial variation of ecological interactions. The early idea that

the strength of biological interactions may be maximized in the tropics and decrease towards higher latitudes (Dobzhansky, 1950; MacArthur, 1972) has triggered recent research into a variety of types of consumer–plant interactions, such as granivory (Moles & Westoby, 2003), florivory (Kelly *et al.*, 2008)

and folivory (Andrew & Hughes, 2005a; Pennings & Silliman, 2005; Adams & Zhang, 2009). At present, the evidence suggests that temperate forests have lower folivory rates than tropical ones (Coley & Aide, 1991; Coley & Barone, 1996; Schemske *et al.*, 2009). This pattern is the result of latitude representing a complex environmental gradient, along which the effects of abiotic variables (e.g. temperature, photoperiod) may have a direct influence on folivores, as well as an indirect one through changes in plants, natural enemies and mutualists (Andrew & Hughes, 2004). Few studies have accounted for the relative importance of plant versus insect regulation on folivory along latitudinal gradients (e.g. Cornelissen & Stiling, 2009).

Variation in folivore density and per capita feeding rate may explain latitudinal patterns in folivory rates (Cornelissen & Stiling, 2009; Pennings *et al.*, 2009). Stressful environments are usually associated with lower growth rates, increased development time and reduced survival and herbivory rates (Whittaker & Tribe, 1996; Williams, 1999). In temperate regions, the latitudinal decrease in temperature may constrain the density of exothermic arthropods because temperature declines below their physiological optimum (Deutsch *et al.*, 2008). Indeed, temperature is identified as the dominant abiotic factor directly affecting insect herbivores (reviewed by Bale *et al.*, 2002), which is also supported by the increase in insect herbivore performance that occurs with an experimental increase of temperature (reviewed by Zvereva & Kozlov, 2006), and the higher folivory rates that occurred during warmer geological periods (reviews by Currano *et al.*, 2008; Wilf, 2008). Nonetheless, Andrew & Hughes (2005b) did not find the expected latitudinal reduction in arthropod herbivore density on *Acacia falcata*, and we found no other study in trees. Thus, quantifying the potential covariation among climate, folivore density and folivory along latitude, as performed in the present study, will help us to understand the controls of folivory and the potential effects of climate change.

Folivory may also vary in intensity due to variation in morphological and functional leaf traits (Stamp, 2003), which could be affected by the latitudinal change in several factors (e.g. temperature, photoperiod, rainfall; Wright *et al.*, 2005). At evolutionary scales, slow-growing plants should be better defended and experience lower herbivory than fast-growing plants (Stamp, 2003; Fine *et al.*, 2004; Agrawal, 2007). Moreover, some adaptations to abiotic stress (e.g. leaf toughness, trichomes) may decrease herbivory as well (Coughenour, 1985; Coley, 1987; Agrawal, 2007). Some studies have shown that, in spite of lower folivory at higher latitudes, defences are generally lower and/or palatability is higher in high-latitude plant species (Coley & Aide, 1991; Coley & Barone, 1996; Pennings *et al.*, 2001; Hallam & Read, 2006) or conspecific provenances (Pennings & Silliman, 2005). This defence/palatability pattern was therefore suggested as the selective response of plants to herbivory levels, rather than being a causal factor controlling latitudinal herbivory gradients (Pennings *et al.*, 2001, 2009; Hallam & Read, 2006; Schemske *et al.*, 2009). At present, it is unclear how latitudinal changes in leaf traits may relate to folivory levels for the same tree species (Adams *et al.*, 2009), as is the possible influence of climate in moulding this relationship.

Previous studies on trees in temperate and subtropical regions have found contrasting latitudinal patterns of folivory at the intra-specific level. Kozlov (2008) reported the expected decrease in folivory rates on *Betula pubescens* from 60 to 70°N in Europe, but he found no pattern in *Betula pendula* from 48 to 60°N. Andrew & Hughes (2005a) found no latitudinal pattern in *Acacia falcata* in Australia (26 to 35°S), whereas Adams & Zhang (2009) found an increase in folivory rates with latitude in *Acer rubrum*, *Fagus grandifolia*, *Quercus alba* (the three species sampled from 28–30 to 45°N) and *Liquidambar styraciflua* (28 to 41°N) in North America (but see Adams *et al.*, 2009).

In the present study, we used *Nothofagus pumilio* ('lenga') forests from 38 to 55°S as a model system to: (1) assess the spatial pattern of variation in folivory, and (2) understand the influence of climate on herbivory patterns as mediated by changes in folivore density and leaf traits. The latitudinal decrease in temperature may be of special importance in temperate forests, because temperature may be suboptimal for insects at these latitudes (Deutsch *et al.*, 2008). Also, trees experience a cooler environment during the day than other lower-stature vegetation, as they take less advantage of the local ground heating by insolation and experience more cooling through wind movement (Körner, 2007). *Nothofagus pumilio* form monospecific forests along a wide range of latitudes in the Andes of southern South America (Fig. 1a). This setting offers a unique opportunity to analyse the control of folivory at a geographical scale from mid to high latitudes, without the confounding effects of changes in plant species composition.

METHODS

Study plant species

Nothofagus pumilio ('lenga') is a winter deciduous tree that dominates the upper elevational limit of forests in southern Argentina and Chile from c. 35 to 55°S (Fig. 1a). Along most of this region, the Andean mountains form an effective barrier to the westerlies resulting in a pronounced rain shadow. In the northern part of its geographic distribution, the climate is characterized by cold and wet winters and mild but dry summers. Most precipitation falls as rain and snow during autumn and winter, before the main growing season. In the south, precipitation is more evenly distributed within the year (see below; González *et al.*, 2006). *Nothofagus pumilio* ranges from 1300 to 1800 m a.s.l. at the northern end of its geographic distribution, and decreases southward at c. 60 m per degree of latitude, to reach 0–600 m a.s.l. at the southernmost end (Lara *et al.*, 2005). Temperature appears to be an important driver of *N. pumilio* growth at the tree line (Lara *et al.*, 2005). Irrespective of latitude, dominant trees at the lower end of the elevation range attain up to 30 m in height, > 160 cm in diameter at breast height (d.b.h.) and 400 years of age (González *et al.*, 2006). Tree height and d.b.h. show a sharp decrease with elevation, and trees have a shrub form in the krummholz (Barrera *et al.*, 2000).

Sampling design

We sampled 47 *N. pumilio* forest sites from *c.* 38°S to 55°S in the southern Andes of Argentina (Fig. 1a). All sites were chosen to be near the lower altitude limit of this species or near sea level at

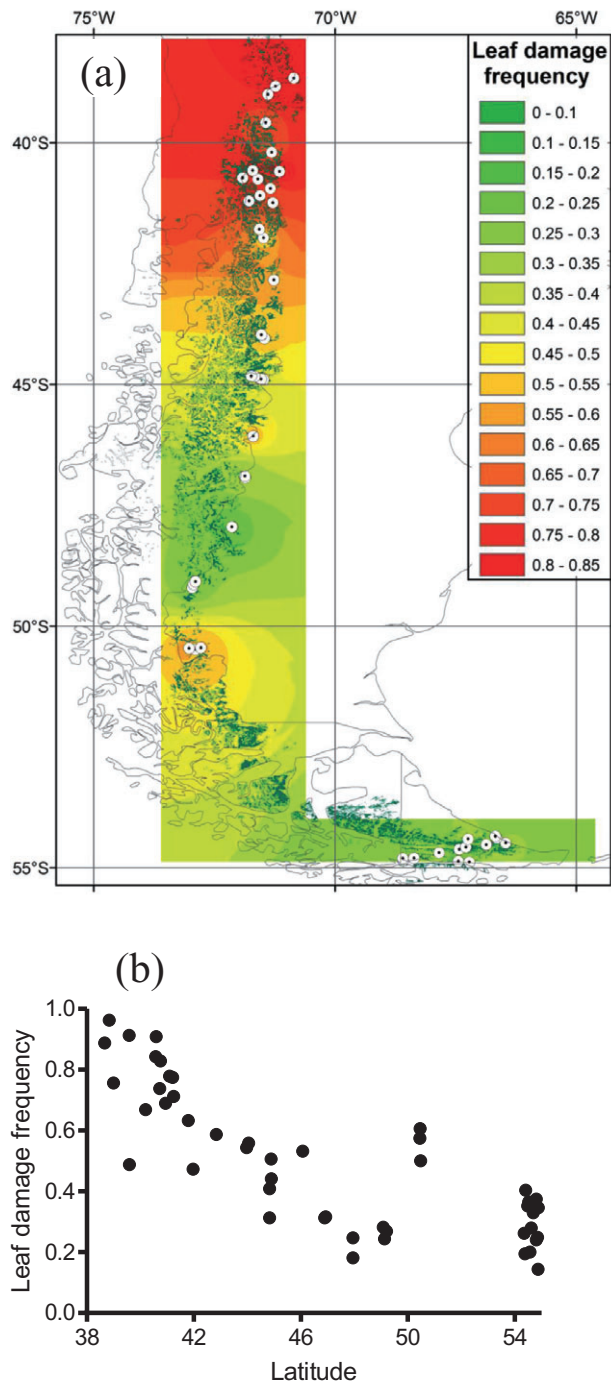


Figure 1 Spatial pattern of variation in leaf damage frequency (summed across all feeding guilds) in *Nothofagus pumilio* forests. (a) Map obtained by inverse distance weighted interpolation (ARCMAP 9.2). The distribution of *N. pumilio* is shown in dark green. (b) Latitudinal variation of leaf damage frequency. In both cases, each dot is a sampled site.

high latitudes (*c.* 54°S) to control for possible elevational effects. *Nothofagus pumilio* was the canopy-dominant species in all sites, and it was the single species in the canopy except at three sites at the northern end of its distribution where *Araucaria araucana* (pehuén) was co-dominant. Selected forest sites comprised a wide spectrum of management practices (e.g. pristine forests, forests within extensive rangelands) and successional states, and we did not narrow our selection by any other criteria (e.g. tree density) than site elevation. In each forest site, we selected 15 adult trees at least 10 m apart from each other, along a 200-m walking transect. Trees of similar size (d.b.h., mean = 68 cm, standard deviation = 21 cm) were selected to compare different sites along the latitudinal gradient. From each tree, we harvested one branch with approximately 400 leaves located in the lower three-quarters of the canopy (regardless of branch aspect in the tree or other criteria); thus leaves were obtained from different heights (3–8 m) in different forests (we did not observe a latitudinal trend in forest height). Branches were immediately stored in a plastic bag, located into refrigerators with coolers, transported to the laboratory within 5 days, and stored there in refrigerated chambers. Sampling was performed towards the end of the growing season around March 2007. We also sampled foliage 1 year earlier during March 2006 in a subset of 17 sites at the northern part of *N. pumilio* distribution (from 38 to 44°S), to adjust the measurement protocol and to detect possible inter-annual differences in observed trends.

Insect density and leaf damage

We measured insect density and leaf damage for different foliage feeding guilds after sampling at the laboratory (Mazia *et al.*, 2004; Garibaldi *et al.*, 2010), including insects which fully consume or damage large fractions of the leaf area such as leaf skeletonizers, miners and chewers, phloem-feeding insects such as pit feeders, and gall makers. The most conspicuous folivores belong to the Lepidoptera (Geometridae, Noctuidae, Saturniidae, Heterobathmiidae), Coleoptera (Curculionidae), Hymenoptera (sawflies, Cynipidae) and Homoptera (Psyllidae; Gentili & Gentili, 1988; McQuillan, 1993). We thoroughly searched for folivores by visually inspecting each of the *c.* 6000 sampled leaves per site (400 leaves \times 15 trees) and expressed folivore density per leaf area (100 cm²). Damage produced by each insect guild was measured in 150 fully expanded leaves per site. For each tree (branch), we selected the first five fully expanded leaves (counting from the base of the shoot) from the first two shoots (counting from the base of the branch). For insects whose damage is mainly produced by leaf area consumption (skeletonizers, miners and chewers), we classified the damaged (or missing) area in each leaf into 10 categories. For pit feeders and gallers, we counted the number of holes (< 1 mm²) or galls per leaf, respectively.

We estimated leaf damage as: (1) leaf damage frequency, measured as the proportion of leaves damaged; (2) mean damage per leaf, measured only in damaged leaves and expressed as area (cm² per leaf), number of holes or galls per leaf according to the insect guild (e.g. see Table 1); and (3) total damage, measured as

	Frequency of damaged leaves	Mean damage per leaf†	Total leaf damage†
All folivores†	-0.80***	-0.41**	-0.66***
Pit feeders	-0.70***	-0.55***	-0.72***
Skeletonizers	-0.67***	-0.65***	-0.64***
Miners	-0.61***	-0.07	-0.45**
Chewers	-0.39**	-0.15	-0.27*
Gallers	0.07	0.23	0.08

Significant effects are shown in bold: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

†Damage by skeletonizers, miners and chewers is accounted for as the missing or damaged leaf area, whereas damage by pit feeders and gallers is measured as the number of holes or galls per leaf, respectively. Therefore, the row 'all folivores' contain information of mean damage per leaf and total leaf damage for insects for which damage can be accounted for by measuring area (all folivores except for pit feeders and gallers), but damage frequency is the sum of all folivores (including pit feeders and gallers).

the percentage of leaf area damaged for leaf skeletonizers, miners and chewers, or as the average number of holes or galls per leaf for pit feeders and gall makers, respectively. Therefore, total damage can increase because of higher leaf damage frequency and/or higher mean damage per leaf. Although latitudinal patterns were consistent for the three variables (see Table 1 and Results), we considered leaf damage frequency a better measure for studying geographical differences in folivory, because it is less sensitive to variations among sampling dates within the growing season (as we measured cumulative damage towards the end of the growing season) and because it is the only measure of leaf damage by which to compare different feeding guilds. Leaf damage frequency (and therefore total damage) can increase because of higher folivore density and/or higher per capita folivore feeding rates (except in the case of less mobile folivores such as gall makers).

Leaf traits and vegetation indices

We recorded several leaf traits for March 2007, including tissue concentrations (%) of nitrogen (N), phosphorus (P), potassium (K), water and total phenols. In addition, we measured leaf size, toughness and specific leaf area (SLA). Each variable was measured for a subsample of 40 fully expanded, non-senescent, undamaged leaves. Our insect density measurements confirmed that folivores were active during March (e.g. Table 1), and associations between leaf traits and leaf damage among sites found in our study are consistent with those found in another study along elevational gradients (L.A.G., T.K. & E.J. Chaneton, unpublished), where leaf traits were also measured earlier in the growing season (see Discussion).

Leaves intended for use in the determination of nutrient concentration were stored at air temperature after harvest, dried at 70°C for 72 h and then milled prior to analyses. Leaf N content was determined by the semi-micro Kjeldahl method. Leaf P and K concentrations were measured after humid acid (HNO₃/HClO₄) digestions, and were determined by inductively coupled plasma atomic emission spectrophotometry (ICP-AES). Total phenols were extracted with acetone (70%) and determined by

Table 1 Correlation coefficients (Spearman) of latitude with leaf damage by different insect feeding guilds in *Nothofagus pumilio* forests.

spectrophotometry (720 nm), and concentrations were expressed as mg of gallic acid g⁻¹ of leaf dry weight (Garibaldi *et al.*, 2010).

Leaves for toughness determination (expressed as g mm⁻²) were stored in refrigerated chambers after sampling. Toughness was measured in hydrated leaves clamped between two plates with a 2.74 mm diameter hole as the weight needed to punch a hole through the laminae with a 1.6 mm-diameter steel rod (we employed the pressure set for Pesola® Medio-Line Scales attached to a handy Pesola® scale) (e.g. Ardón & Pringle, 2008). The force was applied in a constant manner with a 90° angle to the leaf surface, and near the centre of the leaf in the space between veins (no leaf veins were punched). Leaf size (cm²) was quantified by measuring leaf length and then using the following equation, size = -0.68 + (0.91 × length) + (0.28 × length²), fitted by least-squares regression based on 2084 *N. pumilio* leaves taken from a range of forest sites ($r^2 = 0.94$). SLA was expressed as leaf area (mm²) per mg of dry weight. For each site, we expressed leaf toughness, leaf size and SLA as the average of the 40 measured leaves.

Finally, we obtained two vegetation indices, the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI), from the MODIS satellite (ORNL DAAC, 2008). We obtained data at 250 × 250 m pixel resolution each 16 days during the 2006–07 growing season (when *N. pumilio* leaves are present) in coincidence with our leaf sampling. Both indices were estimated as the integral for the growing season, and account for the amount of solar radiation intercepted by the forest. These indices are positively associated with forest primary productivity, and are thus expected to covary with folivory and insect densities (Oksanen *et al.*, 1981; McNaughton *et al.*, 1991).

Climate

For each study site, we obtained temperature and precipitation data from the WorldClim database (1 × 1 km pixel resolution, version 1.4, Hijmans *et al.*, 2005). Mean annual temperature from WorldClim was positively correlated with mean tempera-

ture obtained from HOBO H8 loggers (Onset Computer Corporation, MA, USA) during 1 year of measurements in some *N. pumilio* forests (38 to 55°S, $n = 11$, Pearson's $r = 0.67$, $P = 0.02$). Overall, mean annual temperature (data not shown) and the mean temperature of the warmest quarter (the 3 months when trees and folivores are most active), both decreased with latitude (see Appendix S1 in Supporting Information). We found six southern sites (49–50°S) with a higher temperature than expected from the latitudinal trend (Appendix S1). Local atmospheric conditions may differ here due to a stronger influence from the Pacific Ocean given the lower altitude of the Andes. Temperature seasonality also decreased at southern forest sites (Appendix S1). On the other hand, both mean annual precipitation and precipitation seasonality decreased with latitude (Appendix S1). This pattern differs from that on the western slopes of the Andes where precipitation increases from north to south, but also becomes more equitably distributed over the year to the south (Miller, 1976). Precipitation trends are consistent with current knowledge about climatic conditions in our study region, but absolute values reported by WorldClim were lower than those reported elsewhere for specific sites or regions (Barros *et al.*, 1983; González *et al.*, 2006).

Data analyses

Detection of geographical trends

We studied the correlation of leaf damage, folivore density and leaf traits with latitude using Spearman's coefficients because of non-normal distributions. We mapped the spatial pattern of measured variables, for visualization purpose, using inverse distance weighted (IDW) interpolation. IDW estimates cell values using a linear-weighted combination of sample points, where the weight assigned to each cell is a function of the distance of an input point from the output cell location (ARCMAP 9.2).

The spatial pattern in most ecological variables often encompasses broad (e.g. latitudinal) trends along with more patchy (nonlinear) patterns at local scales (Borcard *et al.*, 2004; Bellier *et al.*, 2007). We performed a principal coordinates of neighbour matrices (PCNM) analysis (SAM software, v. 3.0, Rangel *et al.*, 2006) on latitudinally detrended leaf damage frequency to explore the existence of further (non-latitudinal) spatial trends. The PCNM method takes into account the neighbourhood relationships among the sampling sites to derive eigenvector-based spatial filters that account for spatial patterns of autocorrelation in the data set over the whole range of scales encompassed by the sampling design (Borcard *et al.*, 2004; Bellier *et al.*, 2007).

Test of ecological relationships

We used path analysis (Shipley, 2000; R software, v. 2.8, sem package) to test a non-spatial conceptual model of the relationships between environmental factors and leaf damage. Specifically, our model tested: (1) the direct effects of folivore density and leaf traits on the frequency of damaged leaves; and (2) the indirect effects of climate (mean temperature of the warmest

quarter and mean annual precipitation) on leaf damage, as mediated by changes in folivore density or leaf traits. We included in the path analysis only those leaf traits with the highest explanatory power on leaf damage frequency (see Results).

We performed two additional analyses to evaluate the extent to which our ecological model adequately accounted for the spatial autocorrelation in the data. First, we followed Diniz-Filho *et al.* (2003), and elaborated an autocorrelogram of the Moran's I coefficients to compare the spatial pattern of autocorrelation in the observed values of leaf damage frequency, with the pattern in the residuals from the path analysis. If observed values are spatially autocorrelated but residual values are not, the ecological model explained the whole spatial autocorrelation in the data, which suggests that relevant variables were measured and that the ecological model was appropriate. Second, we combined significant spatial and ecological descriptors of leaf damage frequency in a partial regression to partition its variation into: (1) local variation explained by environmental variables independently of spatial autocorrelation in the data; (2) broad-scale variation accounted for by the latitudinally structured component of the environment; (3) spatial variation in leaf damage not shared by the selected environmental variables; and (4) unexplained variation (Borcard *et al.*, 1992). This partition was performed with r^2 indices from the following least-square regressions: (1) leaf damage frequency as a function of spatial predictors and environmental variables selected in the path analysis ($a + b + c$); (2) leaf damage frequency as a function of the environmental variables ($a + b$); and (3) leaf damage frequency as a function of spatial predictors ($b + c$). Then, the proportion of variation (r^2) attributed to each component was estimated as follows: $b = (a + b) + (b + c) - (a + b + c)$, $a = (a + b) - b$, $c = (b + c) - b$ and $d = 1 - (a + b + c)$.

RESULTS

The frequency of damaged leaves decreased with latitude on *N. pumilio* forests (Fig. 1a,b). A subset of sites ($n = 17$) at the northern range of the *N. pumilio* distribution (between 38 and 44°S, Fig. 1a) also showed a latitudinal decrease in leaf damage frequency (Spearman's $r = -0.53$, $P = 0.035$, data from March 2006). Leaf area damaged and mean damage per leaf by all folivores (except for pit feeders and gall makers) also decreased with latitude during March 2007 (Table 1), and showed the same directional but not significant trend during March 2006 (leaf area, Spearman's $r = -0.25$, $P = 0.3$; mean damage, Spearman's $r = -0.08$, $P = 0.7$). Geographical patterns were also evident from variance component analysis, as differences among forest sites accounted for 12% of the variation in leaf area damaged during March 2007, whereas differences among trees within forests accounted for 5% (R software, v. 2.8, lme4 package). The remaining 84% was explained by variation among leaves within trees within forests.

The PCNM analysis showed that once the data on leaf damage were detrended by latitude there was no further spatial pattern of autocorrelation ($P > 0.05$). Similarly, leaf damage frequency

	Frequency of damaged leaves	Mean damage per leaf	Total leaf damage
Total folivore density	0.47**	0.12	0.37*
Leaf traits			
Leaf size	0.67***	0.65***	0.57***
Specific leaf area	-0.19	0.21	-0.08
Toughness	0.36*	0.26	0.31*
Phenolics	-0.15	0.15	-0.06
Nitrogen	-0.01	-0.06	-0.05
Phosphorus	-0.38**	-0.39**	-0.30*
Potassium	-0.27	-0.08	-0.11
NDVI	0.07	0.14	0.08
EVI	0.00	0.14	0.00

Significant effects are shown in bold: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.
 NDVI, normalized difference vegetation index; EVI, enhanced vegetation index.

Table 2 Correlation coefficients (Spearman) of leaf damage (summed across feeding guilds) with total folivore density, leaf traits or vegetation indices in *Nothofagus pumilio* forests.

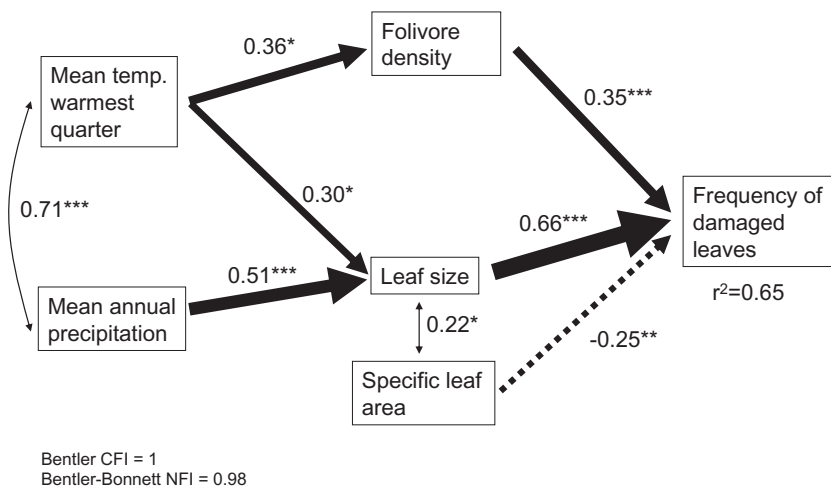


Figure 3 Conceptual model of regulation of folivory rates in *Nothofagus pumilio* forests tested by path analysis. Only significant effects are shown: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Arrow size is proportional to effect size. The dotted arrow indicates a negative effect.

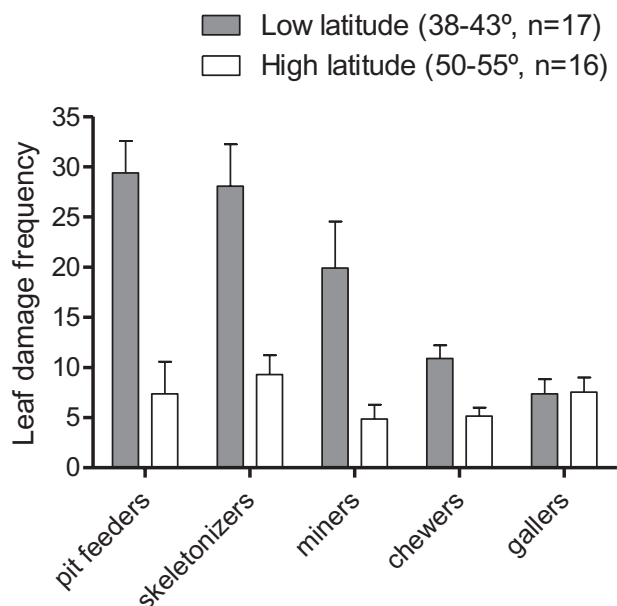


Figure 2 Leaf damage frequency (mean \pm SE) by different insect feeding guilds for northern- and southern-most sites in *Nothofagus pumilio* forests.

did not vary with longitude after controlling for the effect of latitude ($P > 0.05$). Hence, latitude was selected as the only significant spatial predictor to be included in partial regression.

Leaf damage frequency and total leaf damage by pit feeders, skeletonizers, miners and chewers decreased with latitude (Table 1, Fig. 2). These insect feeding guilds also showed a latitudinal decrease in mean damage per leaf, but correlation coefficients were only significant for pit feeders and skeletonizers (Table 1). The only exception to these trends were gall makers, which showed no latitudinal trend in leaf damage frequency, mean damage per leaf or total leaf damage (Table 1, Fig. 2).

Insect density showed a positive association with leaf damage frequency and total leaf damage (Table 2). Accordingly, total folivore density decreased with latitude (Spearman's $r = -0.46$, $P = 0.002$; see Appendix S2). Among leaf traits, leaf size showed the highest correlation with leaf damage (Table 2). Leaf toughness and phosphorus concentration also correlated with leaf damage, while none of the other leaf traits or vegetation indices were associated with leaf damage (Table 2). Based on Akaike's information criterion (AIC), the best linear regression model predicting changes in leaf damage frequency included both leaf size and SLA as explanatory variables (AIC = -35.2, $P < 0.001$).

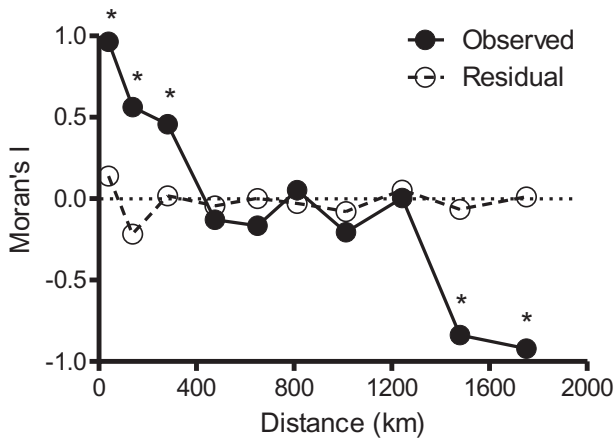


Figure 4 Spatial autocorrelation coefficients (Moran's I) on leaf damage frequency along the latitudinal gradient, and residual (non-explained variation) of leaf damage frequency after the causal model tested by path analysis. *Significant autocorrelation at $P < 0.05$.

Leaf size decreased with latitude (Spearman's $r = -0.66$, $P < 0.001$; see Appendix S3), whereas SLA showed a positive (marginally significant) latitudinal trend (Spearman's $r = 0.27$, $P = 0.07$, Appendix S3). Leaf toughness decreased (Spearman's $r = -0.40$, $P = 0.007$), and phosphorus concentration in leaves increased (Spearman's $r = 0.35$, $P = 0.02$) with latitude.

The path analysis showed significant relationships among the proposed variables (Fig. 3). Mean temperature of the warmest quarter (MTWQ) was positively associated with leaf damage frequency through higher folivore density, whereas mean annual precipitation (MAP) did not covary with insect density (Fig. 3). On the other hand, both MTWQ and MAP were positively associated with leaf damage through bigger leaf size. SLA was negatively associated with leaf damage frequency, but showed no changes with temperature or precipitation. MTWQ and MAP were highly correlated, whereas leaf size and SLA had a significant but weak correlation. Overall, indirect associations of MTWQ on leaf damage [(0.36 × 0.35) + (0.30 × 0.66) = 0.32] were of similar magnitude to indirect associations of MAP (0.51 × 0.66 = 0.34) (Fig. 3).

The ecological model tested by path analysis successfully explained the spatial autocorrelation in folivory (Fig. 4). Moran's I coefficients estimated on the observed frequency of damaged leaves showed spatial autocorrelation, whereas no autocorrelation was found in the residual values of this same variable derived from the path analysis (Fig. 4). Partial regression showed that about 44% of the variation in leaf damage frequency was explained by the latitudinally structured component of environment (component b). The local effect of environmental variables that is independent of latitude accounted for another 22% (component a). Spatial effects not shared by our environmental variables accounted for only 1% of the variation in the leaf damage (component c) and 33% of variation in damage was unexplained by the model (component d).

DISCUSSION

Our study confirmed that folivory, insect density and leaf traits showed significant spatial structure at a geographical scale. Folivory on *N. pumilio* forests decreased with latitude and was associated independently with both changes in folivore density and leaf traits. Climate may play a dual role that involves a control of folivory through its effect on insect density, as well as control by modifying leaf traits. Moran's I coefficients and the partial regression analysis indicated that our results were not seriously affected by the spatial autocorrelation in the data, and that our ecological model adequately accounted for the latitudinal variation in folivory. Spatial pattern of variation was similar for contrasting insect feeding guilds, suggesting no dramatic changes in guild composition across latitude, except for an increase in the relative (not absolute) importance of galling insects at higher latitudes (Fig. 2).

We found that insect density and folivory covaried throughout an extensive number of forest sites (Table 2, Fig. 3), which suggests that variation in folivore density may be an important driver of the spatial variation in herbivory. In agreement, Pennings *et al.* (2009) found that herbivores were more abundant and did more damage to plants at low- versus high-latitude sites of Atlantic Coast salt marshes, but their results varied with the type of herbivore–plant association. In addition, Andrew & Hughes (2005a,b) found no latitudinal trend in insect density or herbivory on *Acacia falcata*. Differences in per capita feeding rates were also found to explain latitudinal variation in herbivory (Pennings & Silliman, 2005; Pennings *et al.*, 2009). Given the scarce evidence on the concurrent latitudinal variation in insect density and herbivory (Pennings *et al.*, 2009), our study contributes with novel information on the consistent broad-scale variation for the same tree species. Further studies are needed to achieve generalization.

Our results suggest that temperature, not precipitation, constrained folivore density to the south and thus folivory rates (Fig. 3). In agreement, the forests with higher than 'typical' folivory at c. 51° S (Fig. 1) were also warmer than their counterparts at high latitudes (Appendix S1). Several studies have reviewed the critical importance of temperature in constraining exothermic insect folivores (Bale *et al.*, 2002; Wilf, 2008), especially in temperate regions (Cornell *et al.*, 1998; Deutsch *et al.*, 2008). Patterns for *N. pumilio* monospecific forests provide evidence of covariation between temperature, insect density and folivory rates without the confounding effects of variation in plant species and insect guild (e.g. Fig. 2) composition. Also, the latitudinal variation in natural enemies or mutualists may constrain insect density among other factors (Whittaker & Tribe, 1996; Andrew & Hughes, 2004). Current studies, however, suggest that the importance of natural enemies may be relatively constant or decrease with latitude (Cornell *et al.*, 1998; Andrew & Hughes, 2005b; Schemske *et al.*, 2009), and the latter should produce the opposite pattern in folivore density to the one we observed. In spite of the latitudinal decrease in intra-annual variability in temperature

and precipitation within *N. pumilio* forests (Appendix S1), our results suggest that cooler mean temperatures at higher latitude reduce the density of insect folivores and the damage they do.

Mechanisms underlying patterns in our study may differ from those proposed for the comparison between tropical versus temperate taxa, or for evergreen versus deciduous plants, as we used a widespread mid- to high-latitude deciduous taxon to analyse latitudinal variation in herbivory. It has been suggested that higher herbivore pressure in the tropics could occur via longer periods of seasonal activity of herbivores (Coley & Aide, 1991; Coley & Barone, 1996). Such an effect would be attenuated for an intra-specific comparison in a deciduous plant like *N. pumilio*, because shorter leaf longevity constrains potentially higher herbivory levels mediated by longer activity periods under favourable (low-latitude) conditions. This effect could be further reduced because most folivore insects in these forests are univoltine (Gentili & Gentili, 1988; McQuillan, 1993). Thus, the possible mechanism for increased herbivory in our study system is reduced mortality at low latitudes, which would increase population densities, rather than per capita feeding (which may actually be reduced by faster development times).

Another possible mechanism operating in *N. pumilio* forests could have been differences in leaf phenology across the latitudinal gradient. However, both leaf bud break and leaf senescence seem to be rather synchronized along this gradient (early October to late April; Rusch, 1993; Barrera *et al.*, 2000; Premoli *et al.*, 2007). This constancy is in agreement with the lack of latitudinal variation in folivore guild composition (e.g. Fig. 2), which suggests that the observed patterns are not the consequence of a phenologically related decrease in leaf availability to certain (early- or late-season) insect guilds.

Leaf size decreased with latitude, and showed the highest correlation with leaf damage among the studied leaf traits and vegetation indices (Table 2). In contrast to other leaf traits such as toughness or secondary chemistry (e.g. Coley & Aide, 1991; Adams *et al.*, 2009), the role of leaf size on the spatial variation in insect herbivory has been poorly explored. Some studies finding lower herbivory associated with smaller leaves concern variation within a tree, or within a habitat; both are conditions where insects have some choice (e.g. Marquis *et al.*, 2002; Low *et al.*, 2009). This differs from the situation where different herbivore populations (separated by hundreds and thousands of kilometres) are faced with leaves of different size (Sinclair & Hughes, 2008). At a geographical scale, forests with small leaves may reduce insect growth rates because of lower foraging efficiency of herbivores (Brown *et al.*, 1991), lower leaf expansion rates (Coley & Kursar, 1996; Kursar & Coley, 2003; Coley *et al.*, 2006) and/or shorter leaf expansion times (Coley & Barone, 1996; Moles & Westoby, 2000). Also, leaf size may be indirectly associated with leaf damage through its covariation with chemical or physical properties of leaves that have a negative impact on herbivory.

Leaf damage covaried with lower SLA, higher leaf toughness and lower phosphorus concentration in leaves at a geographical scale; however, these variables suggest lower quality food for folivores whereas bigger leaves suggest higher leaf quality. Overall, our results show consistent latitudinal variation in leaf traits and folivory, and emphasize the role of leaf size in mediating this association, but more studies will be needed to further understand mechanisms underlying these relationships.

We found that both the lower temperature and precipitation correlated with smaller leaf size but surprisingly not with SLA (Fig. 3), which is commonly reported to increase with decreasing temperature and increasing precipitation (Wright *et al.*, 2004, 2005). There is compelling evidence for the positive influence of temperature and precipitation on leaf size (Wiemann *et al.*, 1998; Reymond *et al.*, 2003; Tardieu *et al.*, 2005), but, to our knowledge there are no previous studies that have associated this variation with folivory rates. Our results suggest that the latitudinal climate variation may be part of the explanation for the observed trend in leaf size and folivory.

The consistent latitudinal variation in leaf size, folivory and folivore density found in the present study suggests that they are part of a common causal scenario, which is also supported by other studies. For instance, in northern Patagonia we found that both insect density and leaf size decreased with folivory rates at higher elevations, and this pattern was also associated with an altitudinal decrease in temperature (L.A.G., T.K. & E.J. Chaneton, unpublished). Also, saplings from high-elevation forest planted in a common environment showed smaller leaf size (Premoli *et al.*, 2007) and higher resistance to folivory (L.A.G., T.K. & Chaneton, unpublished) than saplings from low-elevation forest. In low-altitude forests, there was greater leaf area damaged by chewing insects over 2 years with warm and dry conditions compared with 5 years with average climatic conditions (Mazía *et al.*, 2009). At a local scale, addition of nutrients to *N. pumilio* trees increased leaf size, folivory and folivore density in a dry forest, whereas birds reduced folivore density and folivory rates (Garibaldi *et al.*, 2010).

It has been proposed that the strength of ecological interactions should decrease with latitude (MacArthur, 1972; Pennings & Silliman, 2005; Schemske *et al.*, 2009). We documented a broad-scale decreasing trend in folivory with increasing latitude in *N. pumilio* forests. By using comparable sites and focusing on a single host-plant species we held constant some of the possible confounding variables that influence spatial variation in herbivory, and suggest that climate may be partially governing the strength of this consumer–plant interaction by influencing both plants and herbivores. Thus, predictions of the consequences of climate warming on forest herbivory should consider direct effects on insects as well as alterations of leaf traits that may affect insect performance. We emphasize the value of large-scale analyses of herbivory as complementary to local experimental approaches for understanding the regulation of herbivory.

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SUPPORTING INFORMATION

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

Appendix S1 Latitudinal patterns in temperature and precipitation.

Appendix S2 Latitudinal pattern in folivore density.

Appendix S3 Latitudinal patterns in leaf size and leaf specific area.

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BIOSKETCHES

Lucas A. Garibaldi is interested in the spatial and temporal variation in the strength of plant–animal interactions and the environmental factors and mechanisms (top-down, bottom-up) driving this variation.

Thomas Kitzberger is a scientific researcher for the National Research Council of Argentina (CONICET) interested in the effects of climate and biotic interactions on key ecological processes in southern South American temperate forests.

Adriana Ruggiero is a scientific researcher for the National Research Council of Argentina (CONICET) interested in biogeography and macroecology, with special emphasis on the biota of South America.

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