Interannual changes in folivory and bird insectivory along a natural productivity gradient in northern Patagonian forests

C. Noemi Mazia, Thomas Kitzberger and Enrique J. Chaneton


Trophic regulation models suggest that the magnitude of herbivory and predation (top-down forces) should vary predictably with habitat productivity. Theory also indicates that temporal abiotic variation and within-trophic level heterogeneity both affect trophic dynamics, but few studies addressed how these factors interact over broad-scale environmental gradients. Here we document herbivory from leaf-feeding insects along a natural rainfall/productivity gradient in Nothofagus pumilio forests of northern Patagonia, Argentina, and evaluate the impact of insectivorous birds on foliar damage experienced by tree saplings at each end of the gradient. The study ran over three years (1997–2000) comprising a severe drought (1998–1999), which allowed us to test how climatic events alter top-down forces. Foliar damage tended to increase towards the xeric, least productive forests. However, we found a predictable change of insect guild prevalence across the forest gradient. Leaf miners accounted for the greater damage recorded in xeric sites, whereas leaf chewers dominated in the more humid and productive forests. Interannual folivory patterns depended strongly on the feeding guild and forest site. Whereas leaf-miner damage decreased during the drought in xeric sites, chewer damage increased after the drought in the wettest site. Excluding birds did not affect leaf damage from miners, but generally increased chewer herbivory on hydric and xeric forest saplings. Indirect effects elicited by bird exclusion became most significant after the drought, when total folivory levels were higher. Thus, interannual abiotic heterogeneity markedly influenced the amount of folivory and strength of top-down control observed across the forest gradient. Moreover, our results suggest that spatial turnovers between major feeding guilds may need be considered to predict the dynamics of insect herbivory along environmental gradients.

C. N. Mázia (cmazi@mail.agro.uba.ar), Dept de Producción Vegetal, Fac. de Agronomía, Univ. de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina. – T. Kitzberger, Dept de Ecología, Univ. Nacional del Comahue, Quintral 1250, 8400 Bariloche, Río Negro, Argentina. – E. J. Chaneton, IFEVA–CONICET, Fac. de Agronomía, Univ. de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina.

The search for patterns in trophic dynamics is central for understanding how food webs are structured and react to external perturbations. Phytophagous insects are stereotyped as primary consumers whose trophic relations can be strongly affected by environmental heterogeneity in both space and time (Hunter and Price 1992, Hartley and Jones 1997). Nonetheless, the extent to which insect herbivory patterns reflect the simultaneous impact of spatio-temporal forms of environmental variation has received surprisingly little attention (Floyd 1996, Ritchie 2000, Foraker and Hunter 2000). Multi-year studies conducted at contrasting sites along major habitat gradients represent a powerful approach to examine herbivory dynamics in response to biotic and

Large-scale, steep habitat gradients constitute natural scenarios where insect herbivory may drastically vary in response to either plant resources (Price 1992, Herms and Mattson 1992), natural enemies (Fernandes and Price 1992, Preszler and Boecklen 1996, Alonso 1999), or their interaction (Koptur 1985, Hacker and Bertness 1995, Denno et al. 2002). Inspired by food chain theory (sensu Fretwell 1987), mainly the exploitation ecosystems hypothesis (Oksanen et al. 1981, Oksanen and Oksanen 2000), several recent studies have investigated whether insect herbivory changes predictably along productivity and resource gradients (Stiling and Rossi 1997, Fraser and Grime 1997, 1998, Stiling and Mattson 1998, Denno et al. 2002). However, models based on simple energetic constraints have had varied success in predicting invertebrate herbivory (Schaedler et al. 2003), and have been criticised for neglecting the role of environmental variability and within-trophic level heterogeneity in food web dynamics (Strong 1992, Hunter and Price 1992, Persson et al. 1996, Leibold et al. 1997).

Temporal changes in abiotic conditions can markedly affect insect relations with both their food plants and natural enemies (Larsson 1989, Ritchie 2000). Year-to-year climatic variation and extreme events, e.g. droughts, are known to alter plant quality to herbivorous insects (Ayres 1993, Koricheva et al. 1998). Insect performance may be also directly affected by unusual weather conditions, which often account for transient peaks (Mattson and Haack 1987, Ritchie 2000) or declines (Shure et al. 1998) in herbivory. In addition, insects with different feeding modes, such as endophytic vs exophytic leaf feeders, display specific demographic or behavioural responses to changes in resource availability (Price 1992). Thus insect feeding guilds may exhibit differential susceptibility to various plant and stress factors (Larsson 1989, Koricheva et al. 1998, Shure et al. 1998), as well as to being killed by different natural enemies (Hawkins et al. 1997, Moon and Stiling 2002). This within-trophic level diversity may confound aggregate herbivory patterns, as feeding guilds might replace each other across habitat gradients, while also showing divergent responses to climate variation.

There is ample evidence that natural enemies can limit the abundance of phytophagous insects and their impacts on host plants (e.g. Fernandes and Price 1992, Marquis and Whelan 1994, Hacker and Bertness 1995, Turchin et al. 1999). Simple food chain models predict that the magnitude of predation and strength of top-down control on herbivory increase with habitat productivity (Oksanen et al. 1981, Fretwell 1987). Although this idea has gained some support from invertebrate assemblages (Fraser and Grime 1997, 1998, Stiling and Rossi 1997, Denno et al. 2002), few studies so far addressed how insect guild heterogeneity may influence trophic exploitation under changing productivity scenarios (see Sipura 1999, Ritchie 2000, Moon and Stiling 2002). Indeed, models allowing for species turnover within trophic levels predict a wider array of herbivory and predation responses to increased productivity (Leibold et al. 1997). The template/trophic cascade model proposed by Hunter and Price (1992) further suggests that temporal variability may be critical to the realised impact of top-down forces along habitat gradients. Yet, this issue has remained largely unexplored due to the short-term nature of most empirical studies (Ritchie 2000).

We studied the spatial and temporal patterns of insect folivory in Nothofagus pumilio forests extending over a broad-scale rainfall/productivity gradient in northern Patagonia, Argentina. These native forests occur between the Andes and the Patagonian plains along a steep, west-to-east gradient of decreasing precipitation associated with distance from the Andean divide (Veblen et al. 1996). The forest gradient is characterised by varying levels of productivity decreasing eastward, as shown by remote sensing techniques based on satellite imagery (Paruelo et al. 2001). In addition, Patagonian forests occupy a climatically sensitive zone with large interannual variability in rainfall and temperature (Villalba and Veblen 1998), partly driven by the influence of El Nino Southern Oscillation on southern South America (Pittock 1980, Aceituno 1988). This setting offers a natural template where to examine how spatially and temporally changing environmental conditions may together influence trophic dynamics of herbivorous insects feeding on the same host plant species.

The aims of this work were, first, to determine whether predictable patterns of herbivory and predation occur along a natural rainfall/productivity gradient in northern Patagonian forests, and second, to assess the interannual variation in strength of these top-down forces at contrasting forest habitats. We expected herbivory rates from various leaf-feeding insects and top-down effects from insectivorous birds, a major predator guild in the system (Grigera 1982, Jaksic and Feinsinger 1991), to change consistently across forests located at varying distances from the Andes. We also predicted spatial patterns of folivory and predation would be altered by year-to-year climatic variation in a feeding-guild specific way. Our 3-yr study comprised a severe drought period that affected interactions among trees, insects and birds. Repeated observations and experiments allowed us to document the impact of this climatic event on trophic dynamics along the forest gradient. We specifically addressed the following questions: 1) How does foliar damage from different insect feeding guilds vary over the rainfall/productivity gradient? 2) Are spatial patterns of herbivory consistent among years? 3) How does exclusion of insectivorous birds affect folivory levels at opposite ends of the forest gradient? 4) Does top-down...
control from avian insectivores change in climatically contrasting years?

Methods

Study system and field sites

The study was conducted during 1998-2000 along a west-to-east transect crossing Nahuel Huapi National Park (40°45′S, 71°72′W), near Bariloche, Argentina. In this region the Andean cordillera sets an effective barrier to the westerlies, resulting in a pronounced eastward rainshadow. At the latitude of study, and over a distance of only 60 km, annual precipitation declines from >3000 mm near the divide to <800 mm on the eastern foothills (Barros et al. 1983, Veblen et al. 1996). Above 1000 m a.s.l., native forests are dominated by the tall canopy tree forming extensive monospecific stands from the Valdivian rainforests in Chile through the drier forest zones in Argentina. Forest soils are poorly developed Andisols originated from volcanic ashes; depth of recent ash deposits varies from 2 m in the west to <0.10 m in the east (Veblen et al. 1996).

In March 1998, we selected N. pumilio stands at three contrasting positions along the west-to-east forest gradient, between 1050 and 1200 m altitude. Two sites were chosen at Paso Cordoba (40°36′S, 71°05′W), ca 60 km east of the Andean divide, where total rainfall is ca 1000 mm yr⁻¹. The intermediate gradient position was represented by two sites located 35-40 km away from the Andes, one in Cerro Bayo (40°47′S, 71°35′W) and the other in Cerro Lopez (41°06′S, 71°33′W), both with ca 1800 mm yr⁻¹ rainfall. Finally, we selected one site at Paso Puyehue (40°37′S, 71°50′W) on the border between Chile and Argentina, with ca 3000 mm yr⁻¹ rainfall. Limited accessibility and logistics prevented us from establishing another site on the wettest end of the gradient. The three locations on the forest gradient will be hereafter referred to as “xeric”, “mesic” and “hydric”.

The selected forest zones differ considerably with regard of above-ground primary production as estimated by the Normalized Difference Vegetation Index (NDVI) derived from NOAA/AVHRR satellite imagery (Table 1; see Paruelo et al. 2001, Jobbágy et al. 2002). For the study transect, NDVI measurements for the period (Fig. 1). The 1997-1998 season was humid (March–February: 940 mm) relative to the last 15 yr (mean ± SD = 776 ± 178 mm). In contrast, the 1998–1999 season was extremely dry (357 mm). The 1998 winter was the warmest of the last 15 yr, and the ensuing summer–autumn period was also very warm and dry (Fig. 1). Total precipitation in 1999–2000 was about twice (683 mm) that for the previous year, although the spring was again fairly dry (58% below average) and warm (+1.7°C), being followed by a humid summer (45% above average).

Tree foliage sampling

Field sampling was conducted in March 1998, 1999 and 2000, towards the end of each of three growing seasons (Fig. 1, hereafter referred to as 1998 through 2000). In each site, we haphazardly selected 10 N. pumilio adult trees (dbh, mean ± SD [n = 50]: 49.2 ± 17.7 cm) from within a 1-ha forest stand. Trees were permanently tagged for use in subsequent years. On each sampling date, we collected one fully insolated (northly oriented) twig from each tree at a height of 5.5 m, using an extensible pole cutter. Loss of several tree tags in Cerro Lopez precluded resampling of this mesic site in March 2000.

Herbivory was quantified for 30 leaves per tree as percentage leaf area damaged by insects, by placing a clear 1-mm² plastic grid over the leaf and recording the area of intact and damaged (or missing) tissue. The number of damaged leaves in a sample was used to measure damage frequency per tree. We recorded foliar damage from different insect guilds, including chewers, miners, skeletonizers, and gallers (Gentili and Gentili 1988). Leaf-chewing insects included exophytic caterpillars (Lepidoptera) and weevils (Coleoptera, Curculionidae) (e.g. Bauerle et al. 1997). The most conspicuous chewers in the system are the larvae of Orniscodes cinnamomea (Saturniidae: Hemileucinae), a native moth undergoing periodical outbreaks (Veblen et al. 1996). Larvae hatch in December from overwintering eggs and
develop through several instars feeding on tree foliage until February/March. Leaf mines in *N. pumilio* are produced by *Heterobathmia* spp. (Lepidoptera, Heterobathmiidae). Adult miners oviposit during November and early December and by late January (mid summer) larval feeding has been completed. At the time of sampling, leaves in all forest stands were fully expanded, but not senescing, and most foliar damage had already taken place (Bauerle et al. 1997, unpubl.). Thus, intersite differences in leaf phenology, a potentially confounding factor in comparative field studies (Hunter 1992, Mopper and Simberloff 1995), were not deemed to bias our herbivory measures across the gradient. Here, damage levels represent cumulative folivory within each growing season, reflecting both insect abundance and consumption.

To further characterise differences among forest sites we recorded several foliar traits on tagged trees. Mean leaf size (area, cm²), toughness (g mm⁻²) and water content (% fresh mass) were measured in early March for 30 fresh leaves/tree in each site and year. Toughness was measured as the weight needed to punch a hole through the leaf using a 3 mm-diameter steel rod. Foliar N and P contents (% dry mass) were measured for five composite samples in each site; element concentrations were determined colorimetrically using an Alpkem IV autoanalyser.

**Bird exclusion experiments**

The effect of excluding birds on insect folivory rates was evaluated during the 1998–1999 and 1999–2000 seasons at two *N. pumilio* sites located on the xeric (Chall-Huaco Valley; 41°8’12”S, 71°8’12”W) and hydric (Paso Puyehue) ends of the gradient. The commonest insectivores in the system are the thorn-tailed rayadito (*Aphrastura spini-cauda*, Furnaridae) and the white-crested elaenia (*Elaenia albiceps*, Tyrannidae). Both are medium-sized species (body length ≈ 15 cm) that feed preferentially on canopy insects (Grigera 1982) and are widely distributed across Andean forests (Grigera et al. 1996, Deferrari et al. 2001).

In late spring 1998 (December), we selected in each forest site 20 *N. pumilio* saplings ranging 1–1.5 m in height (2–3 cm basal diameter). Bird exclusion cages were established on 10 randomly chosen saplings, while

Table 1. Characterisation of *Nothofagus pumilio* forests at three contrasting locations along the west-to-east rainfall/productivity gradient in northern Patagonia, Argentina. Data shown are means ± SE for each location.

<table>
<thead>
<tr>
<th>Site location on forest gradient</th>
<th>Hydric</th>
<th>Mesic</th>
<th>Xeric</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Annual NDVI</strong></td>
<td>0.691 ± 0.016</td>
<td>0.648 ± 0.008</td>
<td>0.494 ± 0.018</td>
</tr>
<tr>
<td><strong>Tree-ring width (mm yr⁻¹)</strong></td>
<td>2.6 ± 0.5a</td>
<td>1.4 ± 0.3b</td>
<td>1.2 ± 0.2b</td>
</tr>
<tr>
<td><strong>Foliage traits</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf size (cm²)</td>
<td>3.6 ± 1.2a</td>
<td>3.2 ± 1.0b</td>
<td>2.5 ± 0.9c</td>
</tr>
<tr>
<td>Toughness (g mm⁻²)</td>
<td>40.4 ± 1.2a</td>
<td>40.6 ± 1.0b</td>
<td>67.1 ± 0.8b</td>
</tr>
<tr>
<td>Water content (%)</td>
<td>61.4 ± 1.6a</td>
<td>57.0 ± 1.1b</td>
<td>52.3 ± 0.9b</td>
</tr>
<tr>
<td>Nitrogen (%)</td>
<td>2.14 ± 0.05</td>
<td>2.07 ± 0.04</td>
<td>2.07 ± 0.07</td>
</tr>
<tr>
<td>Phosphorus (%)</td>
<td>0.27 ± 0.004a</td>
<td>0.18 ± 0.005b</td>
<td>0.19 ± 0.009b</td>
</tr>
</tbody>
</table>

*NDVI = Normalised Difference Vegetation Index obtained from NOAA/NASA satellite Pathfinder AVHRR land database (James and Kalluri 1994). Values represent 5-yr (1995–2000) averages of annual NDVI for an 8 × 8-km scene centered on each forest site. The NDVI estimates the fraction of photosynthetically active radiation absorbed by vegetation and derives from satellite measurements of red and near infrared light reflectance (see Paruelo et al. 2001, Jobbagy et al. 2002).

†Tree ring-growth data (1997–2000, December 2001) were analyzed by repeated-measures ANOVA (site × year: F₄,₃₆ = 2.18, p < 0.10), and leaf nutrient contents by one-way ANOVA. Measures of leaf size, toughness and % water represent 3-yr averages (1998–2000) analysed by two-way ANOVAs (see text for full statistics). Superscript letters indicate significant differences among sites (p < 0.05).
the other 10 plants were left uncaged. Saplings within a site were at least 2 m apart from each other, being scattered over 2 ha of undisturbed forest. Cages were 2 m (height) \times 1 m (diameter) in size, and were constructed of wire-mesh wrapping (hole size: 2.5 cm) supported by 2 m-high iron rods. This mesh size effectively excluded insectivorous birds, while still allowing free access to other insect natural enemies such as spiders and parasitoids. The cages had a minor effect on light levels (PAR reduction < 5%) and had no measurable impact on air temperatures. This is not surprising given that the experiments were conducted under closed-canopy micro-habitat conditions. Also, the cages were large enough to avoid any physical interference with sapling growth during the time frame of study.

The bird exclusion experiments were started shortly after leaf flushing so that initial foliar damage on saplings was negligible. In early March 1999 and 2000, before foliage started changing colour, we collected 30 leaves per sapling to assess the percentage leaf area damaged by chewing and mining insects. By this late time of summer, foliar damage produced by both feeding guilds had already levelled off. We took special care to sample leaves from the central zone of saplings in order to minimise any “edge” effect on herbivory measures.

Statistical analysis

We performed factorial ANOVA to test for differences in herbivory among sites and years. The analyses were conducted using the General Linear Models procedure of SAS with type-III sum of squares (Anon. 1996). Means and error measures were calculated by pooling all trees sampled in each gradient position within a year. This design considered individual trees as the basic unit of analysis and, therefore, it tested for statistical differences among forest “sites” without implying a causal relationship between herbivory and any particular habitat factor. The site \times year interaction was strongly significant for most damage measures, indicating the occurrence of temporally changing patterns of herbivory across forest sites. Post-hoc pairwise comparisons were performed to examine differences among sites within years, using Bonferroni tests adjusting for a fixed number of comparisons (Day and Quinn 1989). A three-way, split-plot ANOVA was used to evaluate the effect of excluding birds on leaf damage for xeric and mesic forest saplings. The site and year of study entered the analysis as unreplicated main plots and the cage treatment as replicated subplot. Because ANOVA revealed strong cage \times year effects on herbivory levels, we compared cage effects between forest sites within each year using Bonferroni tests adjusting for k = 6 pairwise tests/year (Day and Quinn 1989). Percent damage data were arcsin-square-root transformed to reduce variance heterogeneity.

Results

Foliage characteristics

Mean leaf size increased westward from xeric, through mesic to hydric forest trees (F2,126 = 26.1, p < 0.0001, Table 1), but did not vary among years (year and site \times year, both p < 0.20). Leaf toughness was higher in xeric than in mesic or hydric sites (F2,126 = 286.7, p < 0.0001) and remained so throughout the study, although toughness levels declined in all three sites during 1999 (year: F2,126 = 153.3, p < 0.0001, site \times year: p < 0.11). Leaf water content increased towards the hydric site (Table 1; F2,126 = 13.8, p < 0.0001). Not surprisingly, leaf water varied among years (F2,126 = 15.9, p < 0.0001), mainly because it decreased in xeric sites with the 1999 drought (site \times year: F4,126 = 6.7, p < 0.0001). Foliar N showed no significant difference across forest sites (F2,11 = 0.5, p < 0.63), while P content was higher in the hydric forest (F2,11 = 60.4, p < 0.0001, see Table 1).

Patterns of insect herbivory

Total insect damage changed significantly among sites and years (Table 2). The frequency of damaged leaves per tree ranged 30–70%, being higher in xeric and mesic sites, except for 2000 (Fig. 2). Damage frequency was overall significantly greater in 2000 after the extended drought. Herbivory levels represented, on average, <14% of the leaf area. However, leaf area damage varied as much as 3.3–4.6-fold across sites within any given year, and up to 5-fold among years within a given site. The highest foliar damage occurred in the xeric forest in 1998 and 2000 (Fig. 3), but no significant difference was found in 1999 (site \times year: p < 0.001). After the drought (2000), leaf area damage increased at both ends of the gradient (Fig. 3). We observed little intrannual variation in folivory levels within mesic sites. Leaf miners and chewers accounted for >80% of total insect damage. The amount of herbivory from both feeding guilds varied significantly among forest sites and with the study year (Table 2, Fig. 3). Leaf area damage by miners was much greater in the xeric forest, except for 1999, when damage levels dropped 50% relative to 1998/2000 (site \times year: p < 0.001). Damage frequency by leaf miners showed a slightly different picture, although it also varied widely (10–50%) across sites and years. Mining insects consistently damaged a larger fraction of available leaves in the xeric and mesic sites than in the hydric one (Fig. 2). For mining insects, damage frequency approximates the rate of successful mines initiated by ovipositing adults, without reference to
Damage from leaf-chewing insects did not consistently vary across sites, but changed among years (Table 2). Damage frequency by chewers increased over the study period in mesic and hydric sites (site × year: \( p < 0.01 \)), from 20% in 1998 to 45% in 2000 (Fig. 2). Yet, the leaf area damaged by chewers increased after the drought (2000) only in the hydric forest (Fig. 3, site × year: \( p < 0.05 \)). Insect skeletonizers contributed a small fraction to total folivory during this study. However, skeletonizers also showed a significant peak after the drought, but in the xeric forest (Fig. 3). Leaf-galling insects showed no trend across sites or years, with damage levels remaining < 0.5%. Overall, during the three-year study, chewing insects produced most foliar damage in mesic and hydric sites (Fig. 4), whereas leaf miners accounted for the greater damage recorded in xeric sites (two-way ANOVA on proportional leaf-miner damage, site: \( F_{2,126} = 74.3, p < 0.001 \), site × year: \( p > 0.10 \)).

**Effects of bird exclusion**

Total folivory levels in experimental saplings were in the range of those found on adult trees within the same season, and generally increased from 1999 (2.5–4%) to 2000 (4–9%). Total leaf damage was strikingly similar in hydric and xeric forest saplings, irrespective of year and cage treatment (Table 3). This reflected a compensatory shift in proportional damage caused by chewing and mining insects in each forest site (Fig. 5). Leaf-chewer herbivory on saplings was significantly higher in the hydric site, especially during 2000 (site × year: \( p < 0.015 \)). In contrast, leaf-miner damage was higher on the xeric forest saplings, and did not significantly change between years (see Table 3).

Bird exclusion promoted a highly significant increase in leaf-chewer damage levels, which was equivalent for the xeric and hydric forest sites (Fig. 5, cage × site: \( p > 0.10 \)). However, cage effects on chewer damage and total folivory rates significantly differed between study years (Table 3). The treatment effect became most apparent in 2000, when chewer folivory levels in either forest site were about twice as high for caged saplings as for those open to bird access (Fig. 5). Excluding birds did not consistently affect the amount of leaf-miner herbivory on saplings. However, there was a marginal three-way interaction (see Table 3), suggesting a weak cage effect on leaf miners for the xeric site that changed direction between years (Fig. 5).

**Discussion**

Many studies have documented the trophic relations of endophytic or epiphytic insects along natural habitat gradients (Koptur 1985, Fernandes and Price 1992, Hacker and Bertness 1995, Preszler and Boecklen 1996, Uriarte and Schmitz 1998, Alonso 1999, Denno et al. 2002). In addition, a number of studies focused on the temporal variation of insect herbivory (Faeth 1985, Shure et al. 1998) and of top-down factors acting on phytophagous insects (Floyd 1996, Turchin et al. 1999, Ritchie 2000). In this work, we explicitly linked both sources of abiotic heterogeneity, and thus clearly showed that folivory patterns over broad-scale environmental gradients can be highly variable across years, even for insects feeding on the same plant species. Furthermore, we found that spatial patterns of herbivory and predation not only were affected by a severe drought event, but also depended strongly on the focal insect feeding guild. These results are compatible with Hunter and Price’s (1992) conceptual model emphasising the importance of temporal variability and guild differentiation for...
understanding trophic regulation along habitat gradients (see also Persson et al. 1996, Leibold et al. 1997).

We studied insect herbivory along a natural, composite forest gradient, where rainfall and productivity can

Fig. 2. Frequency of leaf damage (mean ±1 SE) in *Nothofagus pumilio* along a west-to-east rainfall/productivity gradient in northern Patagonia. Means represent all trees sampled for each gradient position within a year. Horizontal lines connect years not differing in foliar damage (p > 0.05). Different letters above error bars denote significant differences among sites within a year (Bonferroni test, p < 0.0066).

be viewed as two major ecosystem drivers (Veblen et al. 1996, Paruelo et al. 2001, see also Price 1992). It must however be noted that several “bottom-up” factors also changed predictably with precipitation geographical distance from the Andes. These comprised various measured leaf traits (Table 1), soil depth, canopy openness, length of growing season and foliar phenology, all of which may directly or indirectly affect forest insects (see Hunter 1992, Shure and Wilson 1993, Mopper and Simberloff 1995, Shure et al. 1998). Therefore, the dynamics of insect folivory reported here should not be interpreted as being the sole consequence of a specific site factor.

Spatial patterns of insect herbivory

Overall folivory levels tended to increase towards the xeric, least productive end of the forest gradient. More importantly, we found a predictable change in feeding guild prevalence across *N. pumilio* forests (Fig. 4). Mining insects caused most foliar damage in xeric sites, whilst leaf chewers prevailed in mesic/hydric sites. The same pattern emerged from the cage experiments, even though in general damage levels for (uncaged) saplings were lower (2–5%) than those for mature trees (2–14%). Such a dominance replacement between insects with different feeding habit may reflect alternate adaptations to cope with natural variation in plant resources and abiotic factors (Price 1992). This result agrees with resource manipulation experiments that show contrasting feeding-guild specific responses to

changes in host-plant quality or stress (Koricheva et al. 1998, Ritchie 2000, Moran and Scheidler 2002). Unfortunately, however, most field studies describing natural dynamics of insect herbivory have focused on a single feeding guild or species, which has limited our ability to account for community-wide patterns of herbivory in terrestrial environments (Hunter and Price 1992). Moreover, food chain models (e.g. Oksanen et al. 1981, Fretwell 1987) inevitably fail to accommodate such spatial complexities, because they do not allow for differential susceptibility to various controlling factors among herbivorous consumers (Polis and Strong 1996, Leibold et al. 1997).

The observed shift in folivory mode was driven by increased leaf-miner activity in xeric sites. This is consistent with the notion that mining insects may be well protected from dessication (Connor and Taverner 1997). It has been proposed that the distribution of endophytic insects may not reflect habitat productivity, but selection for oviposition sites (Price 1992). Although in our case the frequency of mined leaves did not vary as much between mesic and xeric sites, the leaf area damaged by miners was always greater in the xeric forest (Figs 2 and 3). This suggests that large-scale variation in miner herbivory could result from differences in feeding performance as well as ovipositional preferences (cf. Mopper and Simberloff 1995). Trees showing heavy miner damage in xeric sites had smaller and tougher leaves than least damaged conspecifics in wetter sites (Table 1). Yet, toughness may not work as an effective barrier to miners, since colonisation occurs early in the season on newly flushed, softer foliage (Mază unpubl.). Leaf phenology (Hunter 1992, Mopper and Simberloff 1995) and premature abscission (Bultman and Faeth 1986, Connor and Taverner 1997) have been indicated as factors influencing oviposition patterns and larval performance in mining insects. It is thus possible that early flushing and delayed abscission in xeric sites contributed to determine overall differences in miner herbivory across the forest gradient.

Folivory by chewing insects did not differ among sites in two out of three study years. In contrast to mining insects, leaf chewers appeared to be primarily influenced by temporal effects (Table 2). From a bottom-up perspective (Price 1992), and given the contrasting habitats and vegetation traits associated with the forest gradient, the lack of spatial consistency in leaf-chewer herbivory is puzzling. Whether this resulted from compensatory changes between chewer abundance and consumption rates across forest habitats is unknown. When significant spatial differences for leaf chewers did emerge after the drought, highest damage levels occurred in the most productive forest (Figs 3 and 5), where trees had large and softer leaves, with a relatively high nutritional quality compared to trees in xeric sites (see Table 1).

Table 3. Three-way, split-plot ANOVA for the effect of excluding insectivorous birds on levels of leaf area damage experienced by *Nothofagus pumilio* saplings in hydric and xeric sites during 1998–1999 and 1999–2000. Significant effects are shown in bold type.

<table>
<thead>
<tr>
<th>Source</th>
<th>Leaf chewers</th>
<th>Leaf miners</th>
<th>All folivores</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Df</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>74.63</td>
<td>35.56</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>98.90</td>
<td>47.13</td>
</tr>
<tr>
<td>Site × year</td>
<td>1</td>
<td>14.29</td>
<td>6.81</td>
</tr>
<tr>
<td>Subplot (site × year)</td>
<td>36</td>
<td>2.10</td>
<td>0.88</td>
</tr>
<tr>
<td>Cage</td>
<td>1</td>
<td>113.94</td>
<td>43.42</td>
</tr>
<tr>
<td>Cage × site</td>
<td>1</td>
<td>5.21</td>
<td>1.98</td>
</tr>
<tr>
<td>Cage × year</td>
<td>1</td>
<td>29.58</td>
<td>11.27</td>
</tr>
<tr>
<td>Cage × site × year</td>
<td>1</td>
<td>0.33</td>
<td>0.12</td>
</tr>
<tr>
<td>Residual</td>
<td>36</td>
<td>2.62</td>
<td>1.52</td>
</tr>
</tbody>
</table>
Temporal dynamics of herbivory

Folivory levels varied markedly among years and, in general, were highest after the extended drought period. Nonetheless, dominant feeding guilds exhibited contrasting, site-specific temporal dynamics (Figs 2 and 3). Whereas leaf-miner damage in xeric sites dropped during the 1999 drought, to recover afterwards, leaf-chewing insects accounted for the increased damage recorded in the hydric forest after the drought. Interannual folivory changes on adult trees corresponded with those found on xeric and hydric forest saplings, which experienced a two-fold increase between 1999 and 2000 in miner and chewer damage, respectively. Shure et al. (1998) reported qualitatively similar responses to drought from leaf skeletonisers and strip-feeding lepidopterans in an upland oak forest.

Both direct and plant-mediated responses of foliar insects to abiotic conditions may have influenced year-to-year changes in herbivory (Larsson 1989, Ayres 1993, Ritchie 2000). External factors causing severe plant stress have been shown to negatively affect leaf miners in other forest communities (Shure et al. 1998). The decline in leaf area consumed by miners in 1999 suggests that drought conditions reduced their feeding performance and/or survival, perhaps by forcing early leaf abscission during the summer (Veblen et al. 1996; see Bultman and Faeth 1986, Mopper and Simberloff 1995). Whatever the mechanism, the rapid recovery of leaf

miners between 1999 and 2000 indicated that any drought effect was transient. On the other hand, temporal changes in chewer herbivory were consistent with the common observation that droughts often correlate with lagged peaks of insect damage in temperate forests (Mattsson and Haack 1987, Larsson 1989, Price 1992). Low moisture levels and elevated temperatures prevailing from autumn 1998 through spring 1999 may have enhanced leaf-chewer activity in 2000 (Figs 2 and 3). Alteration of insect demographic rates and/or plant nutritional quality have both been invoked to explain such delayed peaks in herbivory (Mattsson and Haack 1987, Larsson 1989, Ayres 1993). That the outburst of chewers damage had taken place only in the wettest forest suggests that local site factors modulated insect responses to climate fluctuation.

**Top-down control on insect folivory**

Cage experiments indicated that insectivorous birds may exert an important regulatory force on tree folivory in these Patagonian forests. Indirect effects elicited by predator exclusion leading to increased herbivore damage on food plants provide evidence for the existence of trophic cascades (Schmitz et al. 2000), but such effects have rarely been documented for phytophagous insects on temperate forest trees (Marquis and Whelan 1994, Forkner and Hunter 2000). Notice that this study was not devised to identify the precise mechanism behind the observed effects of excluding avian predators on insect herbivory. Thus, it must be recognised that differences in folivory between cage treatments may not need result from direct predation effects on insect abundance (see Marquis and Whelan 1994), but could also arise from nonlethal changes in herbivore behaviour (e.g., reduced feeding time, increased migration rate) associated with predation risk (Schmitz 1998). More critically, however, our results suggest that the actual strength of top-down effects from insectivorous birds changed depending on the leaf-feeding guild, and between climatically contrasting years.

Bird exclusion produced weak and variable effects on leaf miners, but increased chewers damage by over 50%, especially after the drought (Fig. 5). These findings stress the importance of focusing on different herbivore guilds when looking at the relative impact of top-down forces along productivity/resource gradients (Sipura 1999, Moon and Stiling 2002, Moran and Scheidler 2002). It has been proposed that leaf miners may be more susceptible to parasitoid attack than to predator-induced mortality (Hawkins et al. 1997). The presence of such “intermediate” invertebrate consumers may complicate the interpretation of herbivory patterns in vertebrate exclusion trials (Tscharntke 1997). Conceivably, inconsistent cage effects as observed for leaf miners in this study (Table 3, Fig. 5) might result from such “hidden” trophic complexities (Polis and Strong 1996). We recognise that other taxa not measured here, e.g. spiders, may be important predators of foliar insects, while also serving as alternative food to birds. Nevertheless, our results indicate that invertebrate predators, if abundant at all, did not fundamentally modify the effect of excluding insectivorous birds on leaf-chewer herbivory. The elevated chewer damage on caged saplings suggests that bird predation could alter the herbivore guild structure across the forest gradient. We hypothesise that, by suppressing leaf-chewing insects, birds increase the prevalence of leaf miners in xeric forest sites (see Figs 4 and 5).

The exploitation ecosystems hypothesis predicts that top-down control on herbivorous consumers should increase along habitat productivity gradients (Oksanen et al. 1981, Oksanen and Oksanen 2000). Thus, we expected bird exclusion would produce a greater increase in folivory on hydric than on xeric forest saplings. But our experiments revealed no significant cage × site interaction on folivory rates (Table 3), indicating that the net strength of top-down effects from insectivorous birds did not vary among forest habitats. Consequently, post-drought differences in herbivory experienced by saplings at contrasting productivity sites (see Fig. 5) could not be simply attributed to bird insectivory. Source-sink models developed by Oksanen (1990) show that trophic exploitation from highly mobile predators such as birds may actually erase local differences in herbivore abundance across spatially heterogeneous landscapes. Furthermore, our work, together with resource-addition field studies (Ritchie 2000, Forkner and Hunter 2000), suggests that bird–insect herbivore interactions along productivity gradients may not conform with models assuming temporally constant environments.

There is much evidence that top-down controls on insect herbivory can be highly variable in time (e.g. Floyd 1996, Turchin et al. 1999) and may sometimes be rather weak (Ritchie 2000, Forkner and Hunter 2000). Our results support this proposal by showing that climate fluctuation and top-down factors may affect herbivory in a strongly non-additive way (Table 3). While bird exclusion did not alter folivory patterns in the drought year, it produced significant effects in 2000 when overall damage levels were higher (Fig. 5). It appears that avian activity on saplings increased once the drought period receded, as insectivorous birds probably tracked down local changes in insect abundance (Deferrari et al. 2001), or were attracted by foraging cues derived from greater foliage damage (Marquis and Whelan 1994, Floyd 1996, Sipura 1999). The temporal herbivory patterns reported in this study show that environmental effects associated with extreme climatic events may rapidly propagate through interactions...
linking adjacent trophic levels. In this way, temporal abiotic heterogeneity may not only constrain the role of top-down forces in food web regulation (Floyd 1996, Ritchie 2000), but may also override the influence of “static” habitat gradients on herbivory.

We conclude that a full understanding of herbivory patterns cannot be attained without consideration of the changing environmental context in which interactions are embedded (Brown et al. 2001). Our work supports the contention that biotic and abiotic sources of heterogeneity interact to control herbivory in terrestrial ecosystems (Hunter and Price 1992). We have shown that annual climatic variation differentially affected endophytic vs exophytic insects across a forest productivity gradient. Thus, accounting for spatial turnovers between major feeding guilds may be crucial to predict insect herbivory along environmental gradients.

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