BIOTROPICA 42(2): 174–179 2010 10.1111/j.1744-7429.2009.00554.x

Seedling Mortality and Herbivory Damage in Subtropical and Temperate Populations: Testing the Hypothesis of Higher Herbivore Pressure Toward the Tropics

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ABSTRACT

Herbivory rates are generally thought to be higher in tropical than in temperate forests. Nevertheless, tests of this biogeographic prediction by comparing a single plant species across a tropical-temperate range are scarce. Here, we compare herbivore damage between subtropical and temperate populations of the evergreen tree *Aextoxicon punctatum* (Olivillo), distributed between 30° and 43° S along the Pacific margin of Chile. To assess the impact of herbivory on Olivillo seedlings, we set up 29 experimental plots, 1.5 × 3 m: 16 in forests of Fray Jorge National Park (subtropical latitude), and 13 in Guabún, Chiloé Island (temperate latitude). Half of each plot was fenced around with chicken wire, to exclude small mammals, and the other half was left unfenced. In each half of the plots we planted 16 seedlings of Olivillo in December 2003, with a total of 928 plants. Seedling survival, leaf production and herbivory by invertebrates were monitored over the next 16 mo. Small mammal herbivores killed *ca* 30 percent of seedlings in both sites. Nevertheless, invertebrate herbivory was greater in the temperate forest, thus contradicting the expected trend of increasing herbivore impact toward the tropics. Seedling growth was greater in subtropical forest suggesting better conditions for tree growth or that higher invertebrate herbivory depressed seedling growth in the temperate forest. Invertebrate herbivory increased toward temperate latitudes while small mammal herbivory was similar in both sites. We suggest that comparison of single species can be useful to test generalizations about latitudinal patterns and allow disentangling factors controlling herbivory patterns across communities.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: broad-latitudinal range; Chiloé Island; Fray Jorge National Park; herbivory gradient; invertebrate herbivory; mammal herbivory.

BIOTROPICA THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Species distributions are constrained by physical, biological and historical factors. Within a given climatic region, one species can interact with many others that may affect its local abundance positively or negatively depending on the type of interaction. Among the antagonistic interactions, vertebrates and invertebrates feeding on plants can severely constrain plant species abundance because herbivores consume vegetative or reproductive plant tissues, thus affecting plant fitness directly or indirectly.

Coley and Barone's (1996) review suggested that the higher number of insect species and larger populations of herbivores in tropical latitude forests could account for the higher herbivory rates that have occasionally been reported for tropical forests compared with temperate forests. The latitudinal trend in this antagonistic interaction is broadly consistent with the idea that less seasonality in the tropics should allow insect herbivores to have multiple generations and feed constantly though the year, in contrast to temperate latitudes where seasonality strongly restricts herbivore activity periods (Andrew & Hughes 2005). A second hypothesis to explain this trend is that increased levels of plant defenses (chemical and mechanical) in the tropics represent a response to higher herbivore pressure. With higher levels of plant defenses, herbivory per plant is reduced but also herbivores tend to consume more plant biomass from several individuals to compensate for lower digestive efficiency. Evidence also suggests that tropical herbivores tend to be more specialized than temperate ones and hence although each species focuses on specific plant secondary metabolites, as a community they are able to detoxify a greater diversity of plant secondary metabolites, thus becoming engaged in a coevolutionary arms-race with their hosts (Dyer *et al.* 2007). As pointed out by Andrew and Hughes (2005), Coley and Barone's (1996) generalization, although widely accepted, is based on data from published studies that (1) used a variety of methodologies to assess herbivory levels; (2) were performed under a broad range of environmental conditions; and (3) compared different plant species with a variety of phylogenetic backgrounds and varied chemical or mechanical defense traits (Landsberg & Ohmart 1989, Coley & Aide 1991). Moreover, these studies often confound strategies between deciduous and evergreen tree species (Hallam & Read 2006). Accordingly, a key test for this hypothesis is to compare herbivory rates in a single broadly distributed plant species, extending from tropical to temperate latitude. This analysis remains to be done (but see Andrew & Hughes 2005, Hallam & Read 2006 for generic and family comparisons in Australia).

Chilean temperate rain forests dominated by *Aextoxicon punctatum* Ruiz et Pav. (Aextoxicaceae) extend along the Pacific coast of southern South America from 30° to 43° S, thus providing a unique opportunity to evaluate hypotheses about the latitudinal trends in herbivory damage. Several studies have confirmed that

Received 22 January 2009; revision accepted 25 May 2009.

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the biota (*i.e.*, birds, lianas, herbs and ferns) associated with these coastal rain forests is very similar throughout their distributional range; although some animal species with little mobility and large home ranges are excluded from the northern outposts of rain forest (Villagrán & Armesto 1980, Cornelius *et al.* 2000). Recent studies have documented that regeneration of *A. punctatum* (Olivillo hereafter) in coastal forest patches of semiarid Chile is concentrated on the forest edge facing the fog, which moves eastward from the Pacific Ocean (del-Val *et al.* 2006), while regeneration in the main range of the distribution of Olivillo is less patchy and associated with the dynamics of small tree-fall gaps (Gutiérrez *et al.* 2008). On average, the density of Olivillo regeneration under the forest canopy is similar (*ca* 10,000 seedlings/ha) in both geographic areas.

In this study we asked three questions about the interaction between Olivillo and its vertebrate and invertebrate herbivores across a large portion of its geographic range in Chile: (1) Does Olivillo seedling survival differ between subtropical and temperate latitudes? (2) Can differences in herbivore pressure account for differences in tree seedling survival between sites? (3) Are herbivory rates higher toward the tropics as predicted from current theoretical and empirical understanding of insect–plant interaction along the latitudinal gradient?

METHODS

STUDY SITES.—The study was carried out at the northern and southern extremes of the distribution of Olivillo-dominated rain forest along the coast of Chile: northern outposts of rain forest are found as isolated patches at 500–600 m asl on the coastal range of Fray Jorge National Park (30°40′ S, 71°30′ W), whereas more continuously distributed forests are found from 34° to 43° S. We sampled subtropical forests in Fray Jorge and temperate forests at 200 m on coastal hills of Guabún Peninsula, Chiloé Island (41.6° S, 73.9° W), encompassing the extremes of the geographic range of Olivillo (Fig. 1). From paleobotanical data, we know that Olivillo forests derived from a widely distributed Tertiary subtropical flora, which extended throughout southern South America from presently arid to subantarctic latitudes. This flora deteriorated during the Quaternary due to the glaciation of high latitudes and aridization in northern Chile and Patagonia east of the Andes, that is the formation of the arid diagonal of South America (Troncoso *et al.* 1980, Villagrán & Armesto 1980, Hinojosa & Villagrán 1997). Consequently, Olivillo forests at subtropical latitudes became gradually restricted to their current locations on the coastal mountain range influenced by oceanic fogs and disrupted from their main range at temperate latitudes in southern South America. In the northern rain forest outposts, fog condensation keeps the humid conditions required for the maintenance of rain forest species, including trees, epiphytes and vines. Olivillo populations are now isolated and surrounded by a semiarid vegetation matrix (Villagrán *et al.* 2004). In contrast, southern populations of Olivillo exhibit a continuous distribution primarily along the Pacific slopes of the coastal range (Smith-Ramírez *et al.* 2007). Such distribution is currently fragmented by anthropogenic activities. The genetic differentiation of subtropical populations of Olivillo from those of the continuous temperate range document the ancient age of the fragmentation driven by climate change (Núñez-Avila & Armesto 2006).

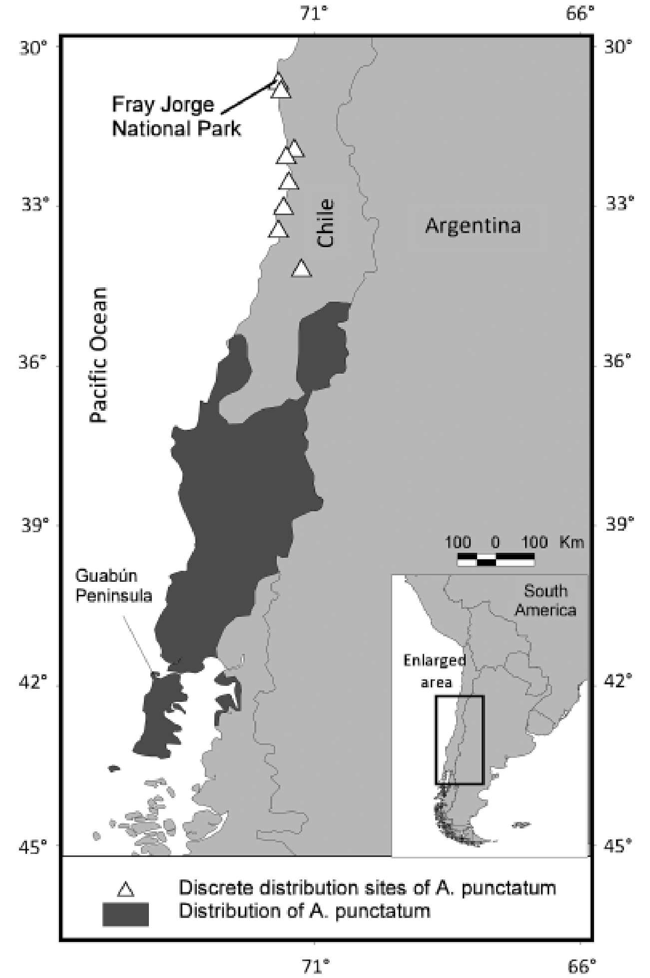

FIGURE 1. *Aextoxicon punctatum* distribution along the southwestern margin of South America, showing discrete and continuous populations. Note there are no populations in the central valley and that populations are largely restricted to the Coastal Mountain range.

In Fray Jorge at 30° S, a mosaic of 180 rain forest patches, ranging in size from 0.1 to 22 ha, occur on the summits (400–600 m) of coastal mountains surrounded by a matrix of semiarid scrub (Novoa-Jerez *et al.* 2004). The regional climate is Mediterranean-arid, with 147 mm (from 21 yr records: 1983–2003) of annual rainfall concentrated in the cool winters (Di Castri & Hajek 1976). Mean annual temperature is 13.6°C. Precipitation shows large inter-annual variability (CV = 81%), with wetter winters associated with the positive phases of ENSO and dry winters associated with negative phases (Jaksic 2001, Montecinos & Aceituno 2003, López-Cortés & López 2004). Fog dripping through the forest canopy and stemflow may contribute an additional 400 mm of precipitation per year (Barbosa 2005). Rain forest patches are dominated (80–100% basal area) by the evergreen, broad-leaved tree Olivillo, the only member of the endemic family Aextoxicaceae, restricted to southern South America. In addition to Olivillo, rain forest patches contain other broad-leaved evergreen trees, such as *Myrceugenia correifolia* (Myrtaceae), *Drimys winteri* (Winteraceae), *Rhaphithamnus spinosus* (Verbenaceae) and *Azara microphylla* (Flacourtiaceae). Woody vines such as *Griselinia scandens* (Cornanceae), *Sarmienta repens* and *Mitraria coccinea* (both Gesneriacae) and epiphytic ferns (*e.g.*, *Polypodium feullei* and Hymenophyllaceae) are frequent components of the forest canopy in Fray Jorge (Muñoz & Pisano 1947, Villagrán & Armesto 1980, Squeo *et al.* 2004). In addition, tree trunks are covered by a dense coat of mosses, lichens and liverworts reflecting local humidity.

The temperate latitude coastal forest of Guabún Peninsula is a 300 ha old growth forest remnant, following land clearing, located in north-western Chiloé Island, Chile. The prevailing climate is wet-temperate with a strong oceanic influence (Di Castri & Hajek 1976); rainfall occurs throughout the year, but about 70 percent falls in the winter months. The nearest meteorological station in Punta Corona has an annual average of 2444 mm and a mean annual temperature of 10.7°C. Mean maximum and minimum monthly temperatures are 13.8°C (January) and 8.3°C (July), respectively (Gutiérrez *et al.* 2008). This rain forest remnant is representative of the extensive coastal forests that once covered the island landscape (Willson *et al.* 1994, Willson & Armesto 1996). Floristically, this coastal forest has a more diverse canopy of evergreen-broad leaved tree species, such as *Eucryphia cordifolia* (Eucryphiaceae), several Myrtaceous species (*Myrceugenia* and *Amomyrtus* spp.) and Olivillo (Aextoxicaceae), with their branches and trunks profusely covered with epiphytic ferns (*e.g.*, *Hymenophyllum* spp., *Hymenoglosum cruentum*, *P. feullei*) and angiosperms (*e.g.*, Gesneriaceae and Bromeliaceae), many of them shared with forests in Fray Jorge. The vegetation presently surrounding the forest consists mostly of open pasture for livestock, which generally stays in the open pastures.

EXPERIMENTAL DESIGN.—We set up 29 experimental plots (16 in Fray Jorge and 13 in Guabún, Chiloé) of 1.5 × 3 m. Plots were set up under closed canopy in each forest. To exclude small mammals half of each plot was fenced around with chicken wire with a mesh opening of 4 cm. The other half was left open as a control. The wire fence was buried 10 cm into the forest floor to prevent animal tunneling. In each half of the plots we planted, in December 2003, 16 1-yr-old seedlings of Olivillo originated from seeds collected from each site for a total of 928 plants. Seedlings were kept in a shaded house inside individual Jiffy pots (biodegradable pots made out of peat) before planting. Pots contained acidic compost from grape soil and were watered regularly. Once seedlings had one or two true-leaves (*ca* 3 mo old), they were simultaneously transplanted to the field without disturbing their roots. In Guabún, current-year seedlings having two true-leaves were collected directly from the forest floor and transplanted into Jiffy pots containing local soil. Seedlings were acclimated inside a shaded house for a period of 3 mo before planting. In Fray Jorge the experimental plots were distributed under the canopy in four different forest patches, two small (*ca* 1 ha) and two large (*ca* 20 ha) patches, while in Guabún, all seedlings were planted in the interior of one large forest patch (*ca* 300 ha), in both sites plots were separated by at least 20 m from each other. Seedlings with their Jiffy pots were planted directly into the forest floor. Every 3 mo and for 16 mo after planting, we recorded seedling growth (leaf production per plant), mortality and leaf damage by invertebrates (estimated as the percent leaf area lost to herbivores per plant, we quantified it as the sum of the percent area lost per leaf divided by the number of leaves per seedling) in both rain forest sites. Seedlings were planted under canopy shade because *Aextoxicon* is known to be a shade-tolerant tree species surviving for several years under the forest canopy (Smith-Ramírez *et al.* 2007).

STATISTICAL ANALYSES.—Seedling mortality was analyzed using a nested ANOVA, on arcsine-transformed percentage of individuals surviving per subplot ($N = 58$) as the response variable. Herbivore exclusion vs. control (−herbivores vs. +herbivores), locality (Fray Jorge, subtropical forest vs. Guabún, temperate forest) and the interaction between herbivore exclusion treatment and locality were the explanatory variables. Locality was also included in the error term to indicate the nested structure of the analysis.

Invertebrate damage to seedlings was assessed for all the surviving plants. For this analysis we calculated the log-transformed percent leaf area lost per plant as the response variable. Locality (subtropical vs. temperate forest) was used as the explanatory variable, and because the number of leaves at the beginning of the experiment differed between localities, this value was included as a covariate. All analyses were performed with the statistical program R (R Development Core Team 2005).

RESULTS

SEEDLING MORTALITY.—Mean Olivillo seedling mortality after 16 mo was significantly higher at the subtropical forest, Fray Jorge, where 43 ± 4.7 percent (mean ± SE) of seedlings survived, than in the temperate rain forest of Guabún, where 66 ± 5.5 percent of all planted seedlings survived ($F_{1, 27} = 11.0$, $P = 0.003$). Herbivory due to the action of small mammals caused significant mortality of Olivillo seedlings in both temperate and subtropical forest ($F_{1, 27} = 38.6$, $P \ll 0.001$). The effect of small mammal exclusions enhanced seedling survival to a similar magnitude in both forests, as the interaction locality × small mammal exclusion was not statistically significant. Mammalian herbivory was responsible for *ca* 30 percent seedling death in both forests (Table 1). Since plants growing in Fray Jorge are distributed in different forest patches and we found that patch size had a significant effect on the levels of seedling herbivory, with seedlings in smaller patches being more affected (del-Val *et al.* 2007), we performed a second analysis considering only seedlings planted in the larger patches in order to remove the effect of patch size. We found the same result, seedling survival was greater in Fray Jorge compared with Guabún ($F_{1, 19} = 4.6$, $P = 0.04$) and Olivillo seedling mortality due to mammalian herbivores was significantly higher than exclosures and of similar magnitude in both sites (herbivore exclusion:

TABLE 1. *Seedling survival (%), leaf area lost per plant due to invertebrate herbivory (%) and number of leaves per plant in experimental plots with and without vertebrate herbivore access (mean ± SE) and ANOVA results for different treatments and their interactions. Values shown are* F *statistics and df are given in parentheses (*$^{*}P < 0.1$; $^{***}P < 0.01$; $^{****}P < 0.001$; *ns = non-significant).*

	Guabún		Fray Jorge		ANOVA		
	With herbivores	W/o herbivores	With herbivores	W/o herbivores	Site	Herbivore exclusion	S × HE
Survival (%)	49.5 ± 7.2	83.2 ± 3.3	30.1 ± 6.1	55.9 ± 5.7	11.0 (1, 27)***	38.6 (1, 27)***	0.54 (1, 27) ns
Leaf area lost per plant (%)	8.9 ± 1.2	8.3 ± 0.8	6 ± 0.9	4.3 ± 0.6	8.9 (1, 472)***	1.41 (1, 472) ns	1.41 (1, 472) ns
No. of leaves per plant	2.9 ± 0.1	3.0 ± 0.1	4.1 ± 0.2	4.6 ± 0.2	98.1 (1, 472)****	3.15 (1, 472)*	1.48 (1, 472) ns

$F_{1,19}$ = 22.0, $P < 0.001$; interaction between site and herbivore exclusion: $F_{1,19}$ = 3.8, P = 0.08).

INVERTEBRATE DAMAGE AND SEEDLING SIZE.—Invertebrate damage to surviving Olivillo seedlings showed an opposite pattern that differed with mortality due to small mammal herbivory. Leaf damage by plant-feeding invertebrates was significantly greater in the temperate rain forest of Guabún than in the subtropical forest at Fray Jorge ($F_{1,473}$ = 9.09, P = 0.003). Excluding seedlings planted in small patches of Fray Jorge also rendered significant results in the same direction ($F_{1,380}$ = 7.78, P = 0.006). Percent leaf area lost to herbivores in Guabún was 8.5 ± 0.7 percent per plant in comparison with 4.9 ± 0.5 percent leaf area lost per plant in Fray Jorge (Table 1). Damage by insect herbivores differed between seedling size ($F_{1,472}$ = 12.7, $P < 0.001$, R^2 = 0.04); larger seedlings with greater number of leaves showed greater leaf damage. Seedlings planted in Fray Jorge had on average a greater number of leaves after 16 mo than those planted in Guabún (4.4 ± 0.1 vs. 3.6 ± 0.1 leaves/plant in Chiloé, $F_{1,472}$ = 98.1, $P < 0.001$; Table 1). This difference was present even though seedling age was similar in both forests.

DISCUSSION

The evolutionary forces experienced by an organism during its lifetime originate from its biotic and abiotic environment. Accordingly, plants and animals with broad latitudinal ranges may experience different selective pressures depending on the location of the population in the latitudinal gradient. In this work, we found that seedlings of a single broadly distributed tree species are subjected to different herbivory depending on the latitudinal location of the forest where tree populations occur. At a subtropical latitude (Fray Jorge), seedlings of the endemic Olivillo showed greater mortality overall, presumably related to harsher environmental conditions (del-Val *et al.* 2006), particularly lower rainfall and higher evapotranspiration rates recorded in forest patches (Barbosa 2005). There is a possibility that differences in seedlings used between Fray Jorge (seedlings grown from seeds) and Guabún (transplanted seedlings) accounted for differences in seedling mortality between sites. Nevertheless, seedlings grew more leaves after 16 mo in the subtropical northern site, compared with plants in the temperate forest of Guabún, Chiloé. This result implies that despite much greater annual rainfall in Guabún, one order of magnitude higher than in Fray Jorge, other abiotic factors (such as light and temperature), differences in transplant procedures or some biotic factors (such as herbivory or pathogen infection) may be restricting seedling growth in the temperate population of Olivillo. However, we should also acknowledge that we did not cover the complete latitudinal distribution of Olivillo, and we only assessed seedling herbivory and survival at the extremes of its distribution; therefore, it is important to take into account that differences in selective pressures toward Olivillo seedlings could be other than just differences in climate (temperature, rainfall, etc.) and differences could also be only related to forest fragment size (larger in Guabún; del-Val *et al.* 2006).

Seedling mortality attributed to the effect of small mammal herbivory after 16 mo was large (*ca* 1/3 of seedlings) and of similar magnitude in both temperate and subtropical populations, since the interaction between latitude and herbivore effects was not significant. Five herbivorous rodent species are probably responsible for seedling mortality in Fray Jorge (del-Val *et al.* 2007), while in the temperate forest of Guabún only one species of rodent is present in significant abundance to be considered a major herbivore (*Abrothrix longipilis*). There is also a small population of deer (*Pudu puda*) and one nonvolant understory bird species that often excavated seedlings after planting (*Scelorchilus rubecula*) and could be causing seedling mortality (Willson *et al.* 1994, E. del-Val, unpubl. data). Interestingly, despite significant differences of mammalian herbivore species between subtropical and temperate sites, their effects on seedling survival did not differ statistically. Therefore, from the tree population perspective, small mammals kill one-third of the seedlings at both latitudes, thus limiting recruitment to a similar level. In contrast to these results, other studies that have assessed mammalian herbivory on forest tree seedlings have found that animals tend to be more discriminatory among tree species toward higher latitudes because seedlings are better defended, given the physiologic and ecologic constraints imposed on seedlings by harsh environments at temperate latitudes. This difference in discrimination seems to have resulted in the evolution of better defenses in arctic plant populations (Swihart & Bryant 2001). We do not know whether defenses of seedlings changed from subtropical to temperate populations, which remains an open and intriguing question.

Assuming that total herbivore damage to plants is always higher in tropical than in temperate latitudes, theoretical and community level studies have argued for long time that the main cause of this pattern is greater insect diversity and abundance in the tropics (Coley & Aide 1991, Coley & Barone 1996). This argument has been generally adopted by plant–herbivore studies but recent field studies have questioned the evidence for the pattern of stronger herbivory pressure in tropical forests. Supporting the original idea, a latitudinal gradient study of Australian Cunoniaceae (Hallam & Read 2006) showed higher concentrations phenolics and declining nutritional leaf quality toward tropical latitudes. Additional support was offered by Progar and Schowalter (2002), who examined insect diversity and abundance across a latitudinal gradient in Douglas fir forests from western United States to find that insect herbivores decreased toward northern temperate latitudes. Nevertheless a study of changes in herbivore pressure on *Acacia falcata* along a latitudinal gradient in Australia showed that herbivory rates did not differ between populations at different latitudes, when considering miners, chewers and sap-suckers (Andrew & Hughes 2005). This pattern is consistent with the review of Landsberg and Ohmart (1989), which documented that *ca* 9 percent of leaf tissue is removed by insect herbivores in all forest types, regardless of latitudinal location. Sinclair and Hughes (2008) study of leaf mining herbivory along a latitudinal gradient in Australia also found no trend across the sampled sites. Pennings *et al.* (2001) experimentally compared plant palatability of several salt marsh species along a latitudinal gradient in eastern United States and found that insects preferred plants from higher latitudes. Results of our study, comparing subtropical and temperate populations of the rain forest tree Olivillo along the Pacific coast of Chile, agree with Pennings *et al.* (2001) results, as invertebrate herbivory on Olivillo seedlings was significantly lower in the subtropical than in the temperate (more austral) population. Because plants in the southern temperate population suffered greater leaf damage from insect herbivores and also produced fewer leaves, we could argue that the selective pressure imposed by invertebrate herbivores to Olivillo is greater in the temperate forest of Guabún, than in the subtropical forest. Nevertheless differences in other environmental factors, particularly access to light under the canopy could also be responsible for the difference in leaf production observed.

It is known that nutrient availability and soil characteristics are correlated with plant tissue quality for phytofagous insects (Coley *et al.* 1985, Boege & Dirzo 2004). In the forests studied, however, Pérez and Villagrán (1994) examined edaphic characteristics (pH, total carbon, total nitrogen, available phosphorous and potassium, % base saturation) along the entire latitudinal range of Olivillo from Fray Jorge to Chiloé Island, documenting striking similarities among coastal forest soils regardless of the distance separating them. Therefore, even though we did not assess leaf chemistry or palatability of Olivillo seedlings to herbivores, differences in leaf consumption are unlikely to be related to differences in soil nutrient availability among sites. Therefore, we propose that documented differences in leaf damage by insects may be related to a different invertebrate fauna (in terms of diversity and abundances). Since the subtropical forest at Fray Jorge is a subset from the vascular plant community present in the continuous main range of Olivillo at higher latitudes, the invertebrate community is probably a subset too. We could also argue that the larger contiguous forest area in Guabún could lead to greater herbivore diversity/damage relative to the smaller fragments at Fray Jorge that are surrounded by a different habitat type (and herbivores not specialized for Olivillo). This would account for lower levels of herbivory in the fragmented subtropical forest patches. These hypotheses warrant further work. After the striking soil and vegetation similarities between forests along the latitudinal gradient, we acknowledge that we need to further work with the Olivillo populations in the middle of its distributional range, in order to find out if the differences in herbivory we found follow a gradient related to latitude or are just differences between two different sites with different environmental conditions.

From our study, the hypothesis about greater insect herbivory rates toward tropical or subtropical latitudes does not hold. Consequently, we suggest that in order to make generalizations about latitudinal trends in herbivory and insect–plant interactions, more comparisons of single species across sites can be useful to disentangle factors controlling herbivory patterns across communities, ecosystems and continents.

ACKNOWLEDGMENTS

We thank Corporación Nacional Forestal (CONAF, IV Región, Chile) for permission to work at Fray Jorge National Park and K. Velázquez for permission to work in the forest of Guabún. J. Monardes, N. Davies, V. Matus, Bernardo González, A. Gutiérrez, and P. Chacón provided generous field assistance. P. Marquet, C. Garín and Y. Hussein shared with us their small mammal trapping data. Pablo Necochea kindly drew the Fray Jorge map. We thank K. Boege and J. Benítez-Malvido for comments on earlier versions. This work was supported by FONDAP – FONDECYT 1501-0001 (CASEB), Biocores Project funded by EC under INCO IV program (Contract ICA 4-CT-2001-10095), CMEB (PO2-051-F), ICM (P05-002) and Project P02-051-F ICM (IEB). This is a contribution to the research program of Senda Darwin Biological Station. The experiments performed for this investigation comply with the current laws of Chile.

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