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Relationship between Exotic Plant Species Richness, Native Vegetation and Climate in Forest Ecosystems of Chile

Pablo I. Becerra and Ramiro O. Bustamante

Abstract

In this chapter, we evaluated how native species cover, native species richness, and foliage periodicity of forests are related to exotic species richness in different forest ecosystems distributed through the Mediterranean-type and temperate climate regions of Chile. We compiled published and unpublished data on Chilean vegetation (mainly phytosociological studies) located between 30° and 41° S in which plant species composition and abundance (percentage of cover) per plot was evaluated and published. When all forests were analysed together, we found that exotic species richness was not significantly related to native species richness; it was negatively related to native species cover in both Mediterranean and temperate climatic regions and was greater in deciduous than evergreen forests, although only in the temperate region. In an analysis considering separately every forest type, we observed that only in 50% of these communities, exotic species richness was negatively related to native species cover. Furthermore, in 25% of forest types, exotic species richness was negatively related to native species richness, and in only one forest type, this relationship was positive. Our results suggest that native species produce some resistance against invasion of exotic plants, but this effect may depend on climate and forest type.

Keywords: alien species, biotic resistance, species diversity, forest communities, plant invasion

1. Introduction

Given the impact of invasive species on native biodiversity, it is important to increase the knowledge about factors influencing invasion processes to establish conservation and restoration strategies [1–3]. Invasion by exotic plant species has been related to biotic (native vegetation and herbivory) as well as abiotic (e.g. climate and soil) factors [3, 4–7]. Among biotic factors, native vegetation has received more attention. Native vegetation may negatively affect invasion of exotic plants through competitive interactions as native species use resources that exotic species also require (space, light, nutrients, etc.) [2, 7, 8]. However, positive effects and facilitation of native species on exotic plants have also been observed [9]. Amelioration of abiotic stress by native vegetation may facilitate recruitment and/or establishment of exotic species, especially under more stressful conditions [10–12]. As a consequence

of these negative or positive interactions, different relationships between native vegetation variables, such as species richness and cover, and invasibility may be expected. For instance, richer communities should reduce niche opportunities for establishing exotic species and hence resist invasion better than poorer communities, and in this case, a negative relationship between native and exotic richness may be expected [2, 7, 13, 14]. This pattern should occur in the absence of covarying extrinsic biotic or abiotic factors [15], which would mainly occur at small spatial scales or within community types [7]. Instead, positive relationships between exotic and native species richness should occur when competition is less important than facilitation [16, 17] or when both, native and exotic species, respond similarly to external environmental factors, which would mainly occur in large spatial scales often including different communities and climates [7]. Empirical evidence shows different results: negative and positive as well as absence of significant relationships have been documented [18–26] although negative relationships have mainly been observed in local scales while positive relationships at larger spatial scales.

Similarly, reductions in native species cover (e.g. by disturbance) would increase plant invasion through depletion of competitive interactions [13, 27]. Many studies have documented that more disturbed habitats, where cover of native plants has been eliminated or strongly reduced, present higher plant invasion [4, 5, 18–20, 25, 28–31]. Nonetheless, it is less clear if within forest habitats, sites with lower cover of native species (e.g. triggered by some natural or anthropogenic disturbance) but without complete elimination of the forest canopy are related to an increase in plant invasion. Alternatively, when facilitative interactions are stronger than competition, positive associations between native and exotic species are more frequent [11], and positive relationships between native species cover and plant invasion may be expected. Moreover, some studies have recently documented invasion in closed-canopy forests by some shade-tolerant exotic plant species [32], and hence for some of these exotic species, greater cover of native species may even be necessary.

On the other hand, the effect of native vegetation on plant invasion may be related to other variables. An attribute of native vegetation, which may affect plant invasion, is the foliage periodicity of dominant tree species (e.g. evergreen and deciduous) [33]. Forest communities dominated by deciduous species receive more light than evergreen forests, at least during a period of time within a year, and thus, evergreen forests may produce greater competitive resistance against plant invasion. However, the role of this factor in plant invasion has been very few times evaluated. Only Ibáñez et al. [33] addressed this issue and documented greater exotic species richness in deciduous forests than evergreen forests in a region of eastern North America.

Plant-plant interactions may strongly be modulated by abiotic conditions [34], and hence, the effect of native vegetation on plant invasion may be influenced by climate or habitat conditions. Specifically, positive interactions should be more frequent under more stressing conditions, while competition under more productive or favourable conditions for plants, which is known as the stress-gradient hypothesis [34]. Although some evidence for this hypothesis has been documented through experimental approaches in the context of plant invasions [10–12, 17], these studies have only been performed at local scales and for particular exotic species. Thus, it is less known that the pattern of relationship between native vegetation variables, such as cover and species richness, and exotic invasion varies between different climatic or habitat conditions according to the stress-gradient hypothesis (but see [25]). Based on the stress-gradient hypothesis, plant invasion should be positively related to cover and richness of native species under more stressing conditions (e.g. arid and semiarid climates), while negatively in more favourable conditions (e.g. temperate climates). Likewise, plant invasion should be greater in deciduous forests than evergreen forests under more favourable conditions.

In this study, we compiled data on exotic species richness at a plot scale in different forest types of Chile and assessed how exotic species richness is correlated to cover and richness of native species, as well as the type of periodicity of foliage of dominant trees in forests distributed through the Mediterranean-type and temperate regions of the country.

2. Methods

2.1 Data source

We compiled several published and unpublished studies on Chilean vegetation, from which we obtained data on exotic and native species composition and abundance at a plot scale from different types of forest communities (**Table 1**). Each one of these communities corresponded to a particular phytosociological unit, most of them at the association level, with homogeneous climate and soil conditions. However, due to differences in geographical distribution among forest types, these had different climatic regimes (Mediterranean-type and temperate climates) and are dominated by species with different periodicity of foliage (deciduous or evergreen). We considered only studies in which species composition and abundance (percentage of cover) per plot were published (e.g. phytosociological tables), from which we obtained values of exotic and native species richness and cover. Within every forest type, selected plots for the analyses had the same size, although the size of plots varied between some forest types. In addition, the distance between plots varied between forest types, from 300 m in some forest types to some kilometres in others. Also, forest types included in the analyses did not show significant evidence (indicated in the publication) of strong anthropogenic disturbances (massive logging of trees or recent fires). This entailed that all plots within each forest types were at least partially covered by a tree canopy. However, forest types could present slight perturbations such as herbivory by exotic livestock and rabbits, tourism impacts (e.g. tracks) and/or reduced past forest logging. This produced a gradient of native species cover and richness within all forests. According to these criteria, we found eight forest types including Mediterranean as well as temperate forests of Chile (**Table 1**).

2.2 Forest types selected for the study

Forest types selected for this study were distributed between 33 and 41°S of Chile, covering both Mediterranean and temperate climates (**Table 1** and **Figure 1**). The most septentrional forest used in this study is a sclerophyllous forest (Becerra, unpublished data), which is an evergreen forest distributed in the coastal range of the semi-arid Mediterranean zone, dominated by the species *Cryptocarya alba* and *Schinus molle*. The Mediterranean montane deciduous forest [35] is dominated by the deciduous species *Nothofagus glauca* and is distributed in coastal as well as pre-Andean foothills of the Mediterranean region. The Mediterranean Subantarctic Andean forest [36] is dominated by the deciduous species *Nothofagus pumilio* and is distributed along the Andean timberline within the humid Mediterranean region of Chile. The temperate montane deciduous forest [37] is dominated by the deciduous species *Nothofagus alpina* and *N. obliqua* and is distributed on the foothills of the Andean range. The swamp deciduous forest [38] is dominated by the deciduous species *Nothofagus antarctica* and is distributed on swamp soils in the central valley of the temperate region. The lowland evergreen forest [38] is dominated by the evergreen species *Eucryphia cordifolia* and *Nothofagus dombeyi* and is distributed on the foothills of the Andean range of

Forest type	Lat.	Long.	Plot (m ²)	N° plots	Region	Foliage	% herbs	% shrubs	% trees
Sclerophyllous forest (Sc)	32°17'	71°11'	100	18	M	E	100	0.0	0.0
Mediterranean montane deciduous forest (Mm)	35–36°	71–72°	100	21	M	D	28.6	42.9	28.6
Mediterranean Subantarctic Andean forest (Sa)	35°35'	71°02'	100	26	M	D	83.3	16.7	0.0
Temperate montane deciduous forest (Tm)	38°26'	71°31'	100	20	T	E	95.0	5.0	0.0
Lowland deciduous forest (Ld)	39–40°	72–73°	140	35	T	D	88.0	12.0	0.0
Swamp evergreen forest (Se)	39–41°	72–73°	100	27	T	E	85.7	7.1	7.1
Swamp deciduous forest (Sd)	40°30'	72°30'	200	10	T	D	90.0	10.0	0.0
Lowland evergreen forest (Le)	41°00'	73°00'	200	10	T	E	90.5	9.5	0.0

Table 1.

Characteristics of the studied forest ecosystems: geographical location or range in which each forest was sampled (latitude and longitude), size of sampling plots, number of plots used, climatic region (M: Mediterranean; T: temperate), foliage periodicity of dominant species (E: evergreen; D: deciduous) and percentages of herb, shrub and tree species in the exotic flora in each forest.

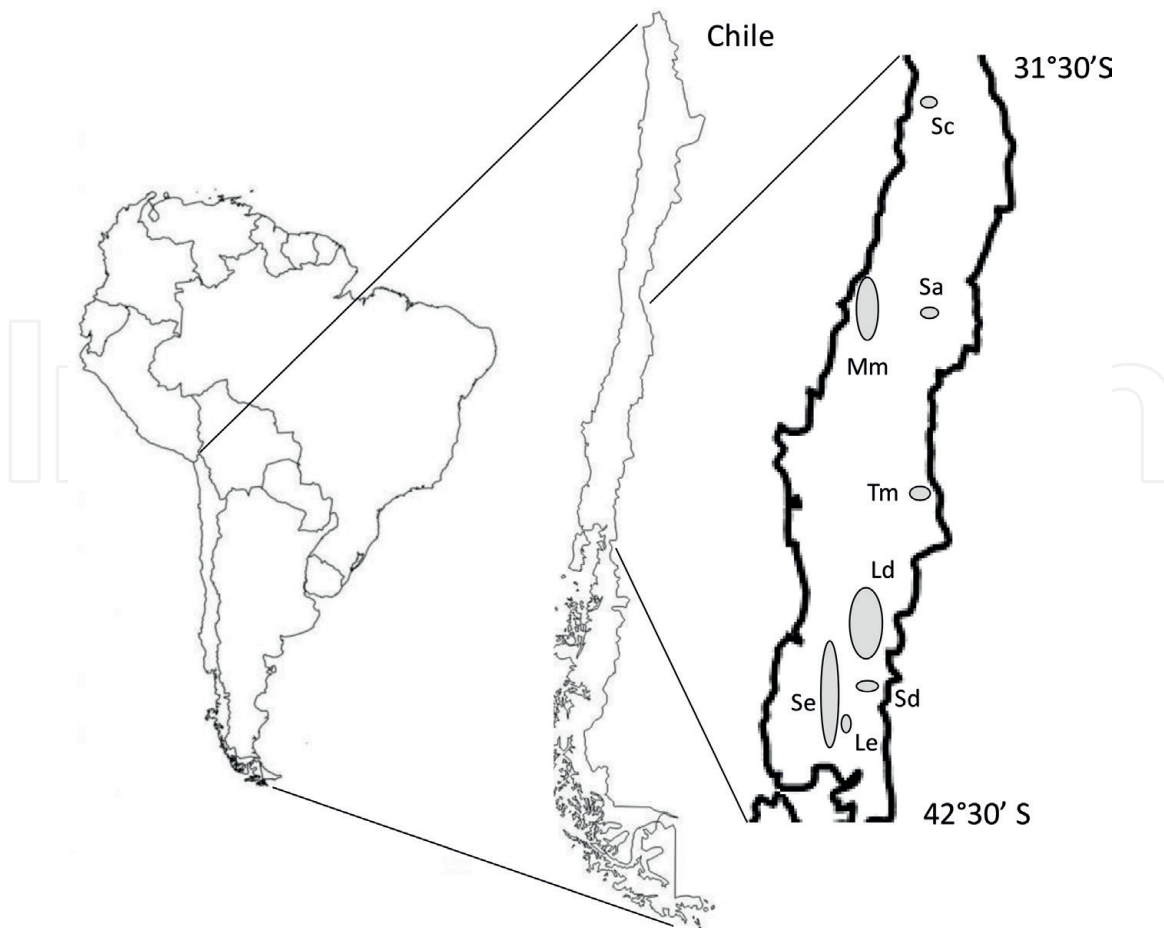


Figure 1. Geographical distribution (only referential location) of forest types included in the study. Different studies covered different surfaces. Nomenclature of forest types is indicated in **Table 1**.

the temperate region. The lowland deciduous forest [39] is dominated by the deciduous species *Nothofagus obliqua* and is distributed in the central valley of the temperate region. Finally, the swamp evergreen forest [40] is dominated by the evergreen species *Myrceugenia exsucca* and *Blepharocalyx cruckshanksii* and is distributed on the lowlands of the temperate region of Chile occupying mainly riverine habitats.

Climate of forests included in this study varied from approximately 350 mm of annual precipitation and an annual mean temperature of 14°C in the sclerophyllous forest, to near 2500 mm of annual precipitation and an annual mean temperature of 10.5°C in the lowland evergreen forest [41].

2.3 Data analysis

We performed two types of analyses: first, we analysed together all data from all forest types, in order to examine the contribution of every variable to the variation in exotic species richness. Thus, in the same model, we evaluated the independent effects of the climatic region (Mediterranean vs. temperate), foliage periodicity of forests (deciduous vs. evergreen), native species richness and native species cover, as well as the statistical interactions between the climatic region and each native vegetation variable. Although the areas of plots were in general quite similar between forests (**Table 1**), the size of plots differed between some of them (**Table 1**), and preliminary $\log_{(10)}$ area- \log (N° species) correlations were significant for all forest types. Hence, to compare exotic and native species richness at a plot scale among all forest types, we controlled the size of plots by dividing values of exotic species richness as well as native species richness by the $\log_{(10)}$ of the area of each plot. On

the other hand, cover values of native species per plot were quantified by the sum of cover among all native species per plot. However, due to larger plots that may have more species and therefore more components for this sum, to use native species cover in the analyses, we controlled the differences in the species number by dividing the sum of cover by the number of native species per plot. Thus, we obtained a variable representing a mean cover of native species per plot.

Finally, we assessed the relationships between exotic species richness and native species richness and cover separately for each forest type with the aim to evaluate if these intra-forest relationships are generalised among different forest types in central-south Chile. In these cases, because within each forest type the size of plots was equal among plots, we did not control the area of them and used the absolute number of exotic and native species as well as the sum of native species cover directly.

All statistical analyses were carried out using SPSS 15.0 by generalised linear models (GLMs).

3. Results

3.1 Exotic flora

Among the eight forest types, we recorded 56 exotic species corresponding to three trees (5.4%), four shrubs (7.1%) and 49 herbs (87.5%). The most common species were *Rumex acetosella* and *Rosa rubiginosa* present in six forest types; *Hypochaeris radicata*, *Prunella vulgaris* and *Veronica serpyllifolia* present in five forest types; and *Anthoxanthum odoratum*, *Holcus lanatus*, *Leontodon taraxacoides*, *Lotus uliginosus*, *Plantago lanceolata*, *Trifolium repens* and *Rubus constrictus* present in four forest types. In general, exotic species were mostly herbs in all forests with percentages greater than 80%, except in the Mediterranean deciduous forest (**Table 1**). Species composition per forest-type is shown in **Table 2**.

3.2 Relationship between native vegetation and exotic species richness

Regarding all forests, exotic species richness varied between 0 and 20 species per plot. After controlling the area of plots, exotic species richness was significantly greater in temperate forests than in Mediterranean forests along all gradients of cover and richness of native species and for each type of forest canopy (deciduous or evergreen) (**Table 3** and **Figures 2–4**). Exotic species richness was negatively and significantly related to the native species cover (**Table 3** and **Figure 2**). This pattern seems to occur in both Mediterranean and temperate forests as we found no significant interaction between the climatic region and native species cover (**Table 3**). However, the slope of this relationship in plots from the temperate region was greater than in plots from the Mediterranean-type climate region (**Figure 2**). In contrast, exotic species richness was not significantly related to the native species richness when all plots were analysed together or in each climatic region separately (**Table 3** and **Figure 3**). On the other hand, exotic species richness was significantly greater in deciduous forests than evergreen forests (**Table 3** and **Figure 4**). Yet, the interaction between region and foliage periodicity was significant (**Table 3**), indicating that higher exotic species richness in deciduous forests than evergreen forests occurred only in temperate forests (**Figure 4**).

When analysing data separately for each forest type, they showed different relationships between native vegetation variables and exotic species richness. A significant negative relationship between native species cover and exotic species

Exotic species	Sc	Mm	Sa	Tm	Sd	Le	Ld	Se
<i>Achillea millefolium</i>				1				
<i>Agrostis capillaris</i>		1		1			1	
<i>Agrostis castellana</i>					1	1		
<i>Agrostis tenuis</i>								1
<i>Anagallis arvensis</i>					1			
<i>Anthoxanthum odoratum</i>				1	1	1	1	
<i>Aster vahlii</i>					1			
<i>Bellardia trixago</i>					1	1		
<i>Bromus hordeaceus</i>			1					
<i>Capsella bursa-pastoris</i>	1							
<i>Cirsium vulgare</i>							1	1
<i>Crataegus monogyna</i>		1						
<i>Crepis capillaris</i>				1				
<i>Cynosurus echinatus</i>				1			1	
<i>Cytisus striatus</i>		1						
<i>Chrysanthemum sp.</i>			1					
<i>Dactylis glomerata</i>				1		1	1	
<i>Digitalis purpurea</i>						1	1	1
<i>Erodium cicutarium</i>	1							
<i>Fumaria officinalis</i>	1							
<i>Galium aparine</i>	1							
<i>Gastroidium ventricosum</i>			1					
<i>Holcus lanatus</i>					1	1	1	1
<i>Hypochoeris radicata</i>				1	1	1	1	1
<i>Lapsana communis</i>				1				
<i>Leontodon taraxacoides</i>				1	1	1	1	
<i>Leucanthemum vulgare</i>						1	1	
<i>Lolium multiflorum</i>							1	
<i>Lolium perenne</i>					1		1	
<i>Lotus uliginosus</i>					1	1	1	1
<i>Medicago polymorpha</i>								1
<i>Mentha pulegium</i>								1
<i>Panicum capillare</i>							1	
<i>Phleum pratense</i>				1				
<i>Pinus radiata</i>		1						
<i>Plantago lanceolata</i>				1	1	1	1	
<i>Poa pratensis</i>				1				
<i>Poa trivialis</i>				1				
<i>Prunella vulgaris</i>				1	1	1	1	1
<i>Ranunculus repens</i>					1	1		
<i>Rosa rubiginosa</i>		1	1	1	1	1	1	
<i>Rubus constrictus</i>					1	1	1	1
<i>Rubus ulmifolius</i>		1						
<i>Rumex acetosella</i>			1	1	1	1	1	1
<i>Salix viminalis</i>								1
<i>Sonchus asper</i>							1	
<i>Stellaria media</i>	1					1		
<i>Taraxacum officinale</i>				1		1	1	

Exotic species	Sc	Mm	Sa	Tm	Sd	Le	Ld	Se
<i>Teline monspessulana</i>		1					1	
<i>Trifolium dubium</i>					1		1	
<i>Trifolium pratense</i>	1					1	1	
<i>Trifolium repens</i>				1	1		1	1
<i>Urtica dioica</i>						1		
<i>Verbascum thapsus</i>				1				
<i>Veronica scutellata</i>						1		
<i>Veronica serpyllifolia</i>			1	1	1	1		1

Table 2.
Exotic species recorded in each forest type. Nomenclature of forests is in Table 1.

Source of variation	Chi ²	P
Climatic region	54.999	<0.001
Foliage periodicity	8.377	0.004
Native cover	5.201	0.023
Native richness	2.241	0.134
Climatic region × foliage	17.278	<0.001
Climatic region × native cover	0.029	0.864
Climatic region × native richness	0.066	0.798

Table 3.
Statistical results (generalised lineal models) for the effect of climatic region (Mediterranean vs. Temperate), foliage periodicity (evergreen vs. deciduous), native species cover and native species richness on exotic species richness (N = 167 plots).

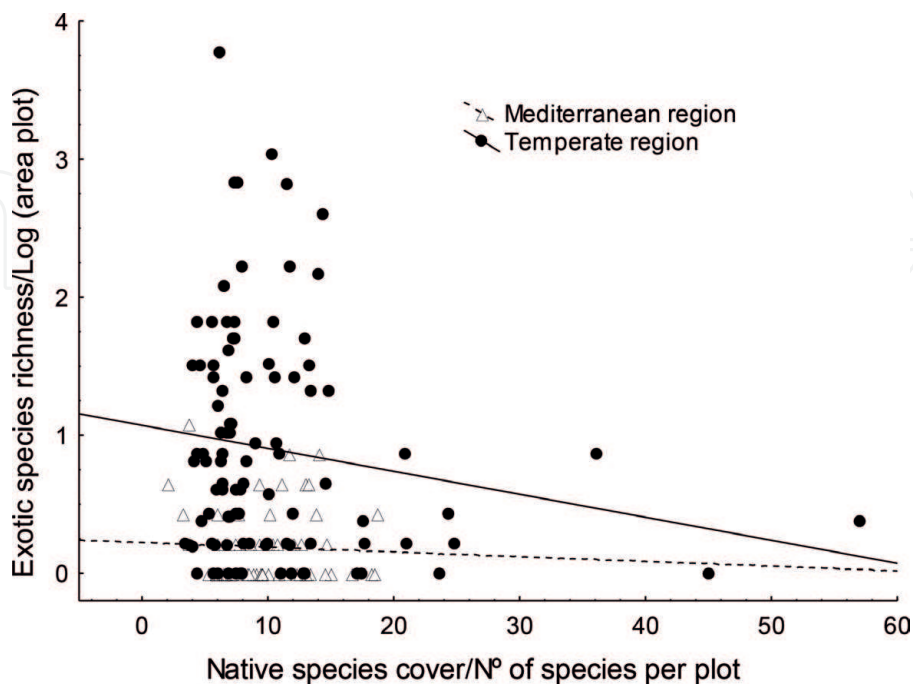


Figure 2.
Relationship between exotic species richness and native species cover per climatic region. Exotic species richness per plot was divided by the logarithm (10) of the area of plots to control the differences of area between plots. Native species cover per plot was divided by the number of native species in the plot to control the differences of richness between plots.

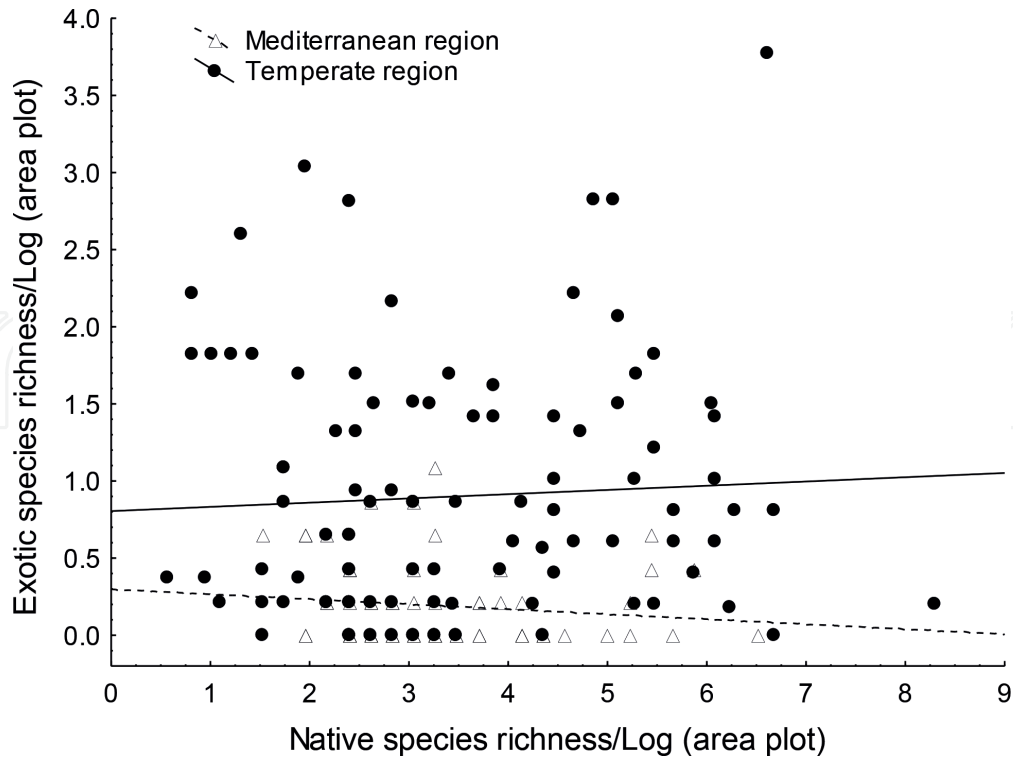


Figure 3. Relationship between exotic species richness and native species richness per climatic region. Exotic species richness and native species richness per plot were divided by the logarithm (10) of the area of plots to control the differences of area between plots.

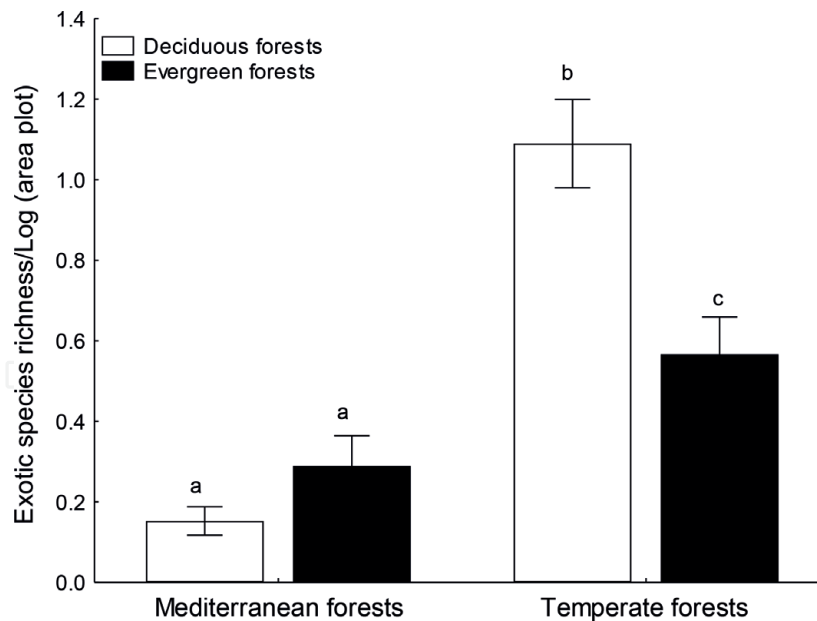


Figure 4. Exotic species richness per climatic region and foliage periodicity type (mean \pm 1 S.E.) ($N = 167$ plots). Different letters indicate significant statistical differences between each combination of region and foliage periodicity ($P < 0.05$).

richness was observed in four forest types, representing 50% of studied forest types, two forests from the Mediterranean-type climate region and two from the temperate region (Table 4 and Figure 5). There was no positive relationship between native species cover and exotic species richness. In turn, a significant relationship between native species richness and exotic species richness was observed only in three forest types, representing 38% of forests included in this study, all of them corresponding

Forest type	Native species richness		Total native cover	
	Chi ²	P	Chi ²	P
Sclerophyllous forest (Sc)	1.901	0.168	0.626	0.429
Mediterranean Subantarctic Andean forest (Sa)	1.217	0.270	7.337	0.007
Mediterranean montane deciduous forest (Mm)	1.043	0.307	8.109	0.004
Lowland deciduous forest (Ld)	11.351	0.001	0.012	0.913
Swamp deciduous forest (Sd)	7.781	0.005	0.550	0.458
Lowland evergreen forest (Le)	0.074	0.786	0.058	0.810
Temperate montane deciduous forest (Tm)	4.526	0.033	11.450	0.001
Swamp evergreen forest (Se)	0.004	0.951	6.160	0.013

Table 4. Statistical results (generalised linear models, ordinal multinomial distribution of data and logit function link) of analyses per forest type for the effect of native species richness and native species cover on exotic species richness. Significant relationships in bold.

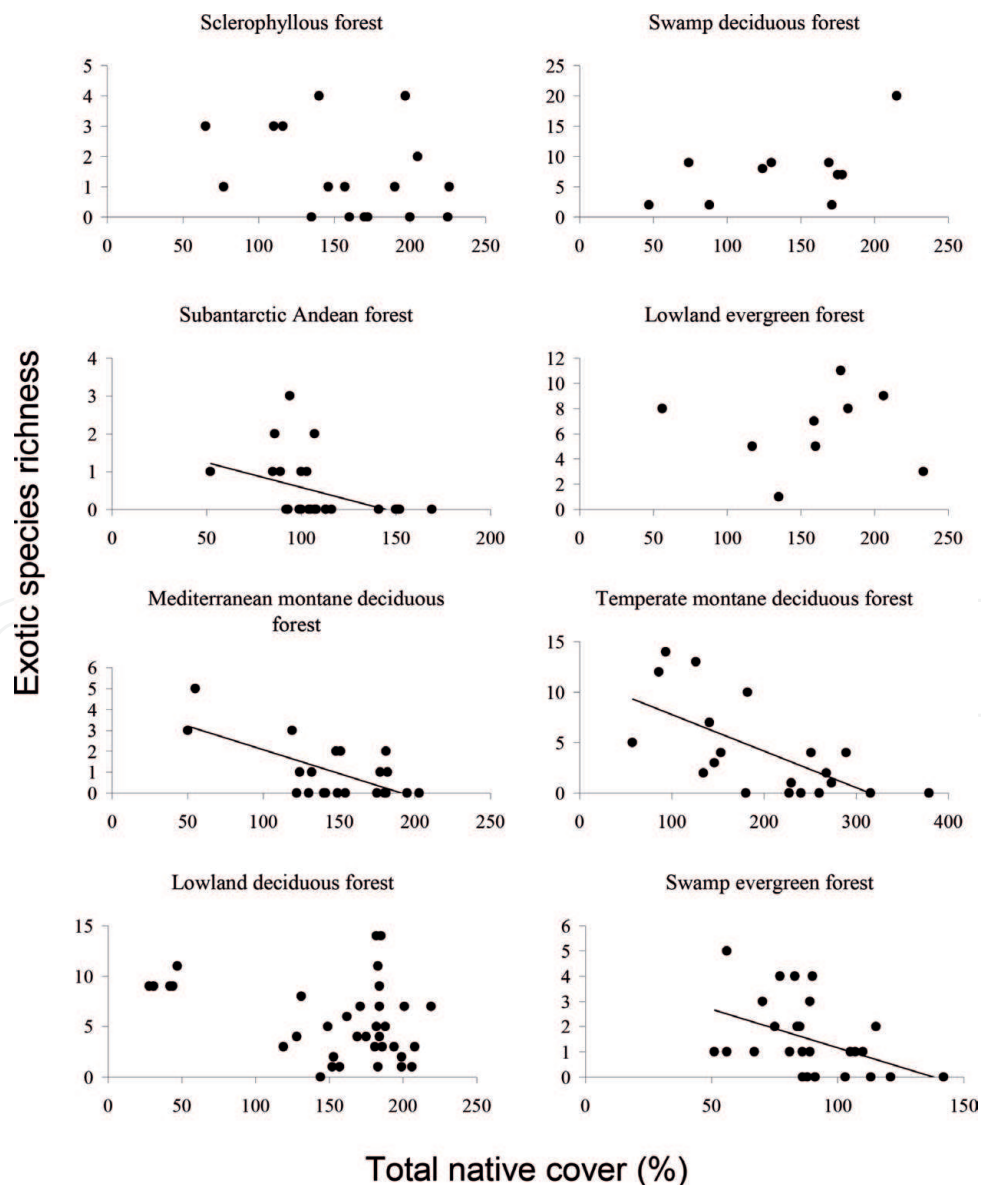


Figure 5. Relationships between exotic species richness and native species cover in every forest type. Curves are shown only for significant relationships.

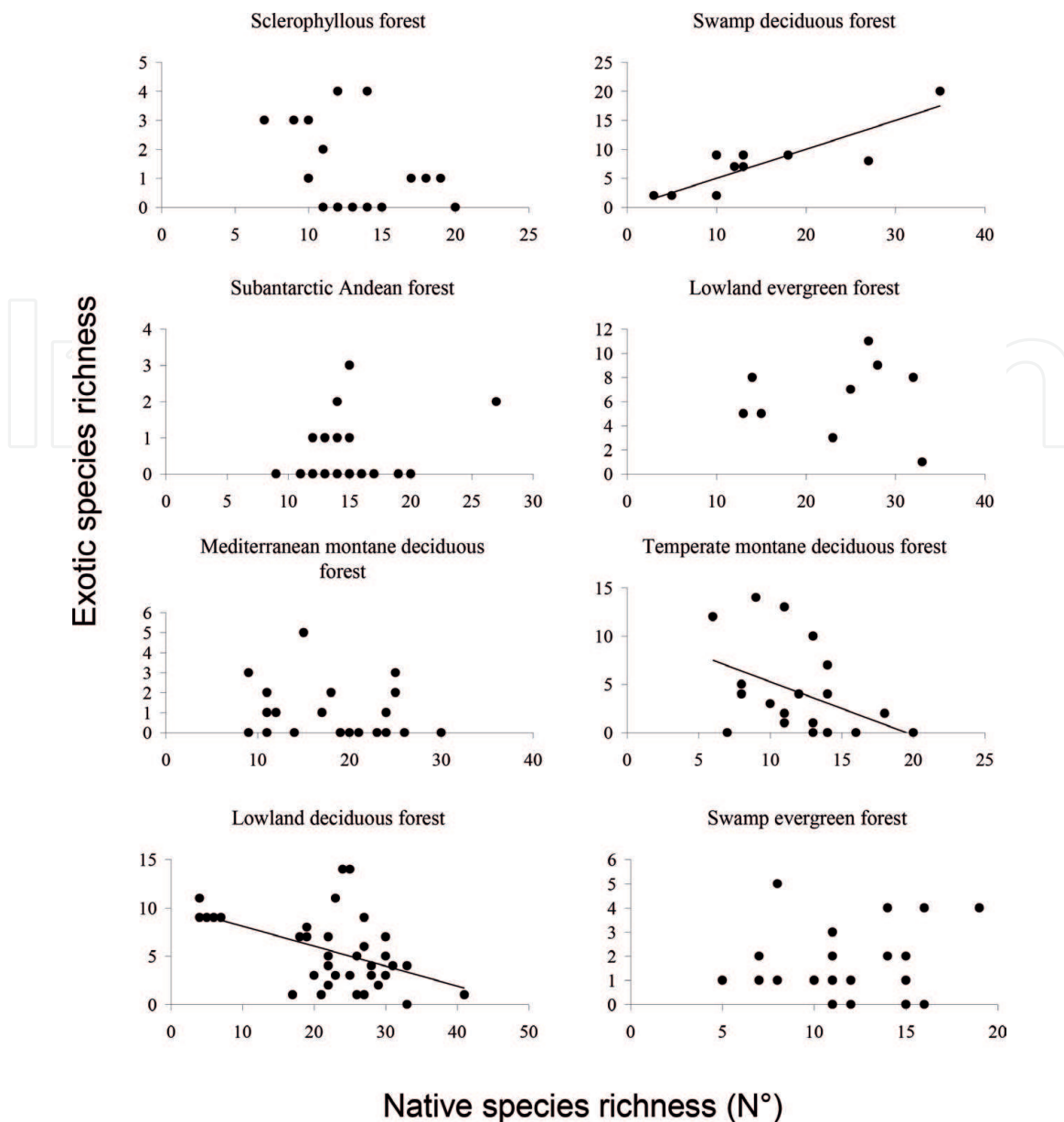


Figure 6. Relationships between exotic species richness and native species richness in every forest type. Curves are shown only for significant relationships.

to temperate forests (Table 4 and Figure 6). However, in this case, in two forests the relationship was negative while in one forest type (Swamp deciduous forest) the relationship was positive (Figure 6).

4. Discussion

In this study, we document that exotic species richness is related to variation in native species cover, foliage periodicity and, at a less extent, native species richness. Additionally, these relationships depend on climate and/or forest type in forest communities of Chile.

The significant negative relationships between exotic species richness and native species cover pooling all forests as well as within some forest types suggest competitive effects of native vegetation on invasion of exotic plants [27]. Variability of native cover within forests may be produced by natural causes (including natural disturbances) as well as anthropogenic disturbances. Regardless of the cause determining this variability, lower native cover entails more resources for invasive species [13, 14, 27]. Therefore, our results suggest a high importance of competition

in invasion processes of exotic species in these forest communities. Similarly, other observational studies performed within forest ecosystems [19, 28, 31, 42] as well as an increasing number of experimental studies have demonstrated the importance of resource availability and competition liberation for plant invasion [8, 12, 21, 23, 43]. Therefore, although many exotic plant species may also invade closed-canopy forests, as documented by Martin et al. [32], our results suggest that more covered sites within or between native forests may better resist plant invasion.

Globally within the study area, we observed no significant relationship between exotic and native species richness. Instead, when every forest was separately analysed, two of them showed a significant negative relationship, which is consistent with the idea that negative relationships between exotic and native species richness would only occur when other factors are controlled (i.e. within each forest type) [3, 7, 15, 21]. This result suggests that, at least in these two forest types, exotic and native species may be competing by resources. However, our results did not agree to Shea and Chesson [7] and some empirical studies [6, 19, 22, 25, 44, 45], which proposed that in geographical comparisons (in our case in the analysis pooling data from all forests), positive relationships between exotic and native species richness should emerge. In particular, the absence of a positive correlation between native and exotic species richness when all forests were analysed together contrasts to Fuentes et al. [26], who found similar geographical tendencies between native and exotic species richness along Chile, although in this case, using much larger scales to measure species richness. Davies et al. [46] proposed that positive relationships between exotic and native species richness would mainly occur when richness is quantified at large spatial scales [26]. This would occur because greater environmental heterogeneity within large quadrants would favour both exotic and native species. Instead, this would not occur at small spatial scales such as a plot-scale (this study), even though plots are compared at a geographical scale [46]. However, Souza et al. [47] found that native and exotic species richness may be positively correlated both at local and landscape scales. Consistent to Souza et al. [47], we observed a positive relationship between exotic and native species richness occurring within a forest type (at a local scale). This positive correlation could be produced by a similar response of native and exotic species to environmental factors [7, 47], or because native species are facilitating exotic species [16, 47]. In the forest type in which this positive relationship was observed (swamp deciduous forest), soil conditions are extreme, with soils permanently saturated with water and low soil oxygen [38]. Therefore, it is probable that within this community, only in microsites (at a scale of 100 m² or less) where soil conditions are a little more favourable, more species, exotics as well as natives, can coexist. Nevertheless, it is not possible to rule out facilitative effects of native on exotic species in this case either.

We observed that in the temperate region, deciduous forests presented greater exotic species richness than evergreen forests, which suggests that the seasonal increase in light conditions in deciduous forests may be a factor contributing to an increase of invasion probability in temperate forests. Higher light requirement of exotic species has been proposed as an important life history attribute favouring the invasion in low-cover sites [14, 43], for instance, ruderal habitats. In fact, most of the exotic species of central-south of Chile have been documented as shade-intolerant species [48]. Although the relationship between foliage periodicity and plant invasion has scarcely been evaluated, our results agree to Ibáñez et al. [33] who documented greater exotic species richness in deciduous forests than evergreen forests in eastern North America. Thus, this factor may be an important driver of plant invasion in forest ecosystems although more studies are needed to assess the generality of this relationship.

On the other hand, our results show that under the same conditions of cover, richness and foliage periodicity of native species, forests from the temperate climate region were richer in exotic species than forests from the Mediterranean-type climate region. This suggests that the Mediterranean-type semiarid region of Chile represents a more stressful condition than the temperate region for exotic species invading forest ecosystems, which agrees to several studies documenting that greater exotic species richness seems to establish mainly in more productive climates [6, 20, 26, 33]. For instance, Lonsdale [6] found a lower number of exotic species in deserts and savannas than in forest habitats around the world, and Stohlgren et al. [20] found a positive relationship between productivity and exotic species richness within North America. Ibáñez et al. [33] documented higher exotic species richness in areas with warmer temperatures and higher summer precipitation in a region of eastern North America. Finally, in the same country, Chile, Fuentes et al. [26] observed greater exotic species richness at a regional scale (10 × 10 km) within Mediterranean and temperate regions than in deserts or colder areas. Nevertheless, in contrast to our results, Fuentes et al. [26] observed higher exotic species richness in the Mediterranean region than the temperate region although, in this case, using larger scales to measure exotic species richness.

If more xeric climates such as in the Mediterranean region of Chile entail more stressful conditions for exotic species (as suggested by the greater exotic species richness in the temperate climate), based on the stress-gradient hypothesis [34], in the Mediterranean region, facilitative interactions and positive relationships may be expected between native vegetation and exotic species richness, while competitive and negative relationships in temperate forests. Thus, the fact that the relationship between native cover and plant invasion was observed in both climatic regions only partially supports the stress-gradient hypothesis [34]. However, the slope of this relationship was steeper in the temperate region than in the Mediterranean-type climate region, suggesting that competitive effects of native vegetation on exotic species were stronger in the less stressful climatic region, which agrees to the stress-gradient hypothesis [11, 34]. Additionally, we did not find a significant negative relationship between native cover and exotic species richness in the most xeric forest included in this study (sclerophyllous forest), which again suggests that under more stressing conditions in terms of water availability, competition would be weaker, or that facilitative effects of native vegetation on exotic species counteracted any competitive interaction (e.g. [10, 12, 17]). Furthermore, two among five temperate forests presented negative relationships between native cover and exotic richness, and in the other temperate forest (lowland deciduous forest), a negative relationship between native and exotic species richness was observed. These results suggest that in temperate forests negative relationships between native vegetation and exotic species are more frequent than in Mediterranean forests, which agree with the stress-gradient hypothesis. On the other hand, the fact that deciduous forests presented greater exotic richness than evergreen forests only in the temperate region suggests that in more humid regions the light conditions may be a more important limiting factor for exotic species than in Mediterranean-type climates. This result may also be consistent with the stress-gradient hypothesis since competition by light would be stronger under less stressful abiotic conditions (temperate region). In consequence, our results suggest that the stress-gradient hypothesis may be useful to predict patterns of relationship between exotic species richness and native vegetation when species richness is analysed at small spatial scales. Other studies [11] have also found support for this hypothesis in the context of interactions between native and exotic species.

Finally, our results suggest that maintaining or increasing native species cover may help to control or reduce plant invasion, at least in terms of exotic species richness. This may be a successful management strategy for the control of invasion mainly in

temperate forests as well as in some Mediterranean-type climate forests. Instead, in more xeric Mediterranean forests (e.g. sclerophyllous forest), an increase in cover of native species does not seem to be enough to reduce exotic species richness, and other actions are needed to control plant invasion.

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