

Do exotic pine plantations favour the spread of invasive herbivorous mammals in Patagonia?

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Abstract Changes in land use patterns and vegetation can trigger ecological change in occupancy and community composition. Among the potential ecological consequences of land use change is altered susceptibility to occupancy by invasive species. We investigated the responses of three introduced mammals (red deer, *Cervus elaphus*; wild boar, *Sus scrofa*; and European hare, *Lepus europaeus*) to replacement of native vegetation by exotic pine plantations in the Patagonian forest-steppe ecotone using camera-trap surveys (8633 trap-days). We used logistic regression models to relate species presence with habitat variables at stand and landscape scales. Red deer and wild boar used pine plantations significantly more frequently than native vegetation. In contrast, occurrence of European hares did not differ between pine plantations and native vegetation, although hares were recorded more frequently in firebreaks than in plantations or native vegetation. Presence of red deer and wild boar was positively associated with cover of pine plantations at the landscape scale, and negatively associated with mid-storey cover and diversity at the stand scale. European hares preferred sites with low arboreal and mid-storey cover. Our results suggest that pine plantations promote increased abundances of invasive species whose original distributions are associated with woodlands (red deer and wild boar), and could act as source or pathways for invasive species to new areas.

Key words: *Cervus elaphus*, invasion, land use change, *Lepus europaeus*, *Sus scrofa*.

INTRODUCTION

Transformation of landscapes by humans may facilitate the spread of invasive species, by changing the spatial and temporal distribution of resources (Sakai *et al.* 2001; With 2002). In general the replacement of native vegetation by exotic conifer plantations, results in an impoverished flora and fauna (Hartley 2002; Brockerhoff *et al.* 2008); however, some species, including some invasives, can benefit from the habitat provided in these altered habitats (Allen *et al.* 1995; Odgen *et al.* 1997). Moreover, synergy among non-indigenous species could facilitate invasions and increase the likelihood of survival and occurrence and magnitude of ecological impact, as predicted under the invasional meltdown hypothesis (Simberloff & Von Holle 1999).

Exotic forest plantations often have been found to favour invasion of exotic species, including plants (Allen *et al.* 1995; Chiarucci & De Dominicis 1995; Odgen *et al.* 1997; Hobbs *et al.* 2003; Ito *et al.* 2004; Paritsis & Aizen 2008), arthropods (Neuman 1979; Bonham *et al.* 2002; Pawson *et al.* 2008), birds (Clout & Gaze 1984; Lindenmayer *et al.* 2002), and mammals

(Barnett *et al.* 1977; Lindenmayer *et al.* 1999). The increased abundance of exotic species in exotic forest plantations may result from increased disturbance, changes in light and soil conditions, changes in land management, and increased availability of certain resources (Bremer & Farley 2010).

In Argentinean Patagonia, exotic fast-growing plantations have been established since the 1970s in the forest-steppe ecotone, strongly promoted by the state (Schlichter & Laclau 1998). There are approximately 80 000 ha of planted forests, mainly *Pinus ponderosa*, and to a lesser degree, *Pseudotsuga menziesii* and *Pinus contorta* (Loguercio & Deccechis 2006; CFI-FUNDFEAEP 2009). A few herbivorous mammal species also were introduced into Patagonia during the late 1800s and early 1900s, mainly for hunting (Grigera & Rapoport 1983; Jaksic *et al.* 2002). The most widespread species are European hare (*Lepus europaeus*), red deer (*Cervus elaphus*), and wild boar (*Sus scrofa*). While these species benefit local economies (Novaro & Walker 2005), they may affect native ecosystems in several ways (Vázquez 2002). Through browsing, grazing and trampling, these species have altered floristic composition and stand structure in Andean rain forests and xeric woodlands (Veblen *et al.* 1992; Vázquez 2002). These introduced herbivores are also suggested to affect native herbivores through

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competition (e.g. *C. elaphus* with the native *Hippocamelus bisulcus* (APN 1992), and *L. europaeus* with *Dolichotis patagonum* (Bonino *et al.* 1997)). Apparent competition could also be affecting native prey species by enhancing the population abundance of predators (Novaro & Walker 2005).

Because pines are mostly planted in areas of Patagonia that were formerly steppe or open woodland, we hypothesized that the presence of these new forests in open areas will favour the abundance of exotic herbivores associated with woodlands in their native habitats (Heptner *et al.* 1966; Mitchell *et al.* 1977), and negatively affect introduced herbivores adapted to open habitats (Flux & Angermann 1990). We tested these hypotheses by (i) examining patterns of habitat use of introduced mammalian herbivores in afforested landscapes, and determining whether the presence of pine plantations in the forest-steppe ecotone modifies local abundances of these species; and (ii) determining which habitat variables at different spatial scales are related with the presence of these introduced mammal herbivores in afforested landscapes. Answers to these questions are important to define management practices of planted landscapes that consider their effects on invasive species.

METHODS

Study area

We conducted this study in the Meliquina Valley (40°28'S, 71°13'W), northwest Patagonia, Argentina. The study area consists of two north-south-orientated intermountain valleys (Meliquina, Filo Huaum – Caleufu rivers), with steep, stony mountain slopes and narrow floodplains. Elevations range from 800 to 2000 m. Climate is temperate to cold, with maximum and minimum annual average temperatures of $17.1 \pm 0.5^\circ\text{C}$ and $4 \pm 2.1^\circ\text{C}$, respectively. Mean annual rainfall ranges between 800 and 1400 mm year⁻¹ (Barros *et al.* 1983).

Native vegetation in the study area consists of a transition between *Austrocedrus chilensis* forest and arid steppe, dominated by bunchgrasses (*Festuca*, *Stipa*, and *Poa* spp.), low shrubs (*Mulinum*, *Berberis*, and *Senecio* spp.), and sparse patches of *A. chilensis* woodlands, accompanied by *Lomatia hirsuta*, *A. chilensis*, *Maytenus boaria*, and *Schinus patagonicus*. In wet microsites and along the borders of creeks, there are patches of shrublands dominated by *Nothofagus antarctica*, a small deciduous tree. This area has been grazed since the beginning of the 20th century. Cattle typically are stocked at low densities and range freely over extensive areas (Funes *et al.* 2006) with no fencing enclosures. Vegetation structure and composition remains similar to the original ecotonal vegetation, although some areas show a reduction of understorey cover and replacement of some herbaceous species, because of overgrazing (Laclau 1997; Funes *et al.* 2006).

The study area holds some of the most extensive forest plantations in the region, with approximately 4350 ha

planted primarily with ponderosa pine (*Pinus ponderosa*) and secondarily with lodgepole pine (*Pinus contorta*) and Douglas-fir (*P. menziesii*). Plantations occur along the slopes and bottom of the river valleys (between 800 and 1200 m a.s.l.), distributed in stands of about 15–25 ha separated from one another by open strips, 30–35 m in width, designed to act as firebreaks. We restricted our investigation to areas >400 m from human settlements, >50 m from major roads, and ≤1 km from any trail or minor road.

Sampling design

We conducted camera-trap surveys to estimate the relative habitat use of introduced species of herbivorous mammals. We established a total of 69 sampling stations in native vegetation, pine plantations, and firebreaks.

Approximately 4200 ha (approximately 50% of the study area) of native vegetation occurred in our study area. We randomly selected 30 sampling stations with native vegetation cover (transition between *A. chilensis* forest and arid steppe, and patches of shrublands dominated by *N. antarctica*), managed using traditional cattle grazing. Twenty of these sampling stations had continuous native vegetation in patches >150 ha in size ≥500 m from the nearest pine plantation. The remaining 10 sampling stations were in native vegetation remnants 5–100 ha in size surrounded by pine plantations.

Selectable conifer plantations represented a total area of 3300 ha (approximately 45% of the study area). We randomly selected 29 sampling stations within ponderosa pine plantations. We selected 20 sampling stations in dense 20- to 28-year-old plantations with complete crown closure and mean tree densities of 800 trees ha⁻¹ located ≥70 m from the plantation edge. We selected the remaining nine sampling stations in sparse pine plantations with mean tree densities of 550 trees ha⁻¹ and crown cover <60%.

We defined firebreaks as strips 30–35 m wide and of variable length between plantation stands established for fire management, where the original vegetation was not replaced by plantations, but was partially removed. Approximately 120 ha of firebreaks (<5%) occurred in our study area. We randomly selected 10 sites in firebreaks.

Habitat description

At the stand scale we characterized the structure and composition of vegetation within 100 m of each sampling station using 25 randomly located 1-m² plots and 10 randomly located 25-m² plots. In firebreaks, the width of the sampling area was limited to the width of firebreak (30–35 m). We visually estimated proportion of bare ground and understorey cover, and identified all understorey species (up to 0.5 m tall) in each 1-m² plot. We visually estimated the total coverage of mid-storey vegetation (0.5–3 m tall) and identified all species in each 25 m² (Elzinga *et al.* 1998). All estimates were carried out by a single researcher to minimize observer bias. We estimated canopy cover with four observations per point at 10 randomly selected points using a convex densiometer. We estimated tree density (trees ha⁻¹), using the nearest-

neighbour method (Cottam *et al.* 1953), measuring the distance to four nearest neighbours of five different trees randomly selected at each site, and recorded diameter at breast height (d.b.h., in centimetres) of each of these trees. In sampling stations with fewer than 50 trees ha⁻¹ we counted all trees within 100 m of the trap station to calculate tree density. For each sampling station we estimated total canopy height using a clinometer, and calculated basal area (m² ha⁻¹) based on mean d.b.h. and tree density.

We used a 1:30 000 scale land-cover map based on a visual classification of two ASTER 15-m resolution georeferenced and orthorectified images (acquired on 4 May 2003 and 28 March 2007) and ground truthing, to characterize habitat at the landscape scale. We established and mapped eight land classifications: *A. chilensis* forest-steppe mosaics, *N. antarctica* shrublands, *N. pumilio* forest, pine plantation, firebreaks, highland vegetation, cliffs, and human settlements. Landscape metrics were calculated using ArcGIS 9.2 (ESRI, Redlands, California, USA) with the Patch Analyst Extension (Rempel *et al.* 2008). We calculated the area covered by each vegetation type, mean patch size for each, and total number of patches of vegetation within 500 m, 1000 m, and 2000 m of the sampling station. We also calculated the distance of each sampling station to the nearest road, river or stream, cliff, and human settlement.

Herbivores sampling

We used camera traps to estimate habitat use by introduced herbivores. Each sampling station consisted of one camera trap, and sampling stations were separated from one another by a minimum of 1 km. We used 32 Leaf River Trail Scan Model C-1 and four Cuddeback Digital Scouting units, consisting of a camera armed with an infrared sensor programmed to shoot when temperature changes. The two camera models were homogeneously distributed across the different habitat types. As all the studied species are mainly nocturnal, we set stations to be active at night (from 8.00 hours to 20.00 hours), including dusk and dawn, which is the period when species are most active. We checked each camera roughly every 15 days. We sampled from December to April in 2007–2008, 2008–2009, and 2009–2010. Each year we deployed 30 randomly selected stations during each of two 60-day sampling periods. Each sampling station was active for two 60-day periods each year. Over the course of our study we sampled 3745 trap-days in native vegetation, 3618 trap-days in pine plantation, and 1270 trap-days in firebreaks.

Data analysis

To reduce the chance of pseudoreplication, we omitted photographs from the camera traps of a given species separated by less than 1 h. We estimated relative habitat use by dividing the number of images of each species at each site by the sampling effort expressed in 10-day intervals. We assumed that detectability among habitat types was constant, based on results found by Lantschner *et al.* (2012) for other species in the same habitat types and with the same methodology.

We compared number of visits of each species between native vegetation, pine plantations, and firebreaks using Kruskal–Wallis tests and Dunn post-hoc tests. We used non-parametric tests as data did not meet normal distribution. We used Mann–Whitney tests to assess whether relative habitat use differed between continuous native vegetation and remnants of native vegetation, and between sparse and dense pine plantations.

We performed logistic multiple regressions to determine habitat characteristics most closely associated with presence of each species. We used presence/absence of each species in each site as the dependent variable, and included habitat variables at stand and landscape scales as independent variables. To evaluate data for spatial autocorrelation (Lennon 1999), we calculated a coefficient *c* that describes the autocorrelation of a variable *x* with lag *r* (Schadt *et al.* 2002). To pre-select variables for inclusion in the models, we performed Spearman correlations between habitat variables and herbivores habitat use, and chose those that were significantly correlated ($P < 0.05$). We also performed Spearman correlations between pairs of habitat variables, and eliminated those that were highly correlated ($r > 0.7$). We performed a backward stepwise multivariate logistic regression analysis with the selected independent variables. We assessed significance of the models using the Wald statistic and employed the Akaike information criterion (AIC) to evaluate alternative models.

RESULTS

Habitat use

We recorded red deer, wild boar, and European hare in all habitat types (Table 1). We recorded red deer 189 times in 58% of the sites, wild boar 129 times in 57% of the sites, and European hare 194 times in 41% of the sites.

The three species differed significantly in habitat use (Fig. 1 – Kruskal–Wallis $\chi^2 = 22.409$, $P < 0.0001$; $\chi^2 = 20.0156$, $P < 0.0001$; $\chi^2 = 15.012$, $P < 0.001$ respectively). Red deer and the wild boar were recorded more frequently in pine plantations (red deer: $z = 4.412$, $P < 0.0001$; wild boar: $z = 3.940$, $P < 0.0001$) and firebreaks (red deer: $z = 3.575$, $P < 0.001$; wild boar: $z = 3.185$, $P < 0.004$) than in native vegetation, whereas habitat use for these species was similar between pine plantations and firebreaks (red deer: $z = 0.426$, $P = 1$; wild boar: $z = 0.374$, $P = 1$). In contrast, the European hare was more frequently recorded in firebreaks than in native vegetation ($z = 3.947$, $P < 0.0001$) or pine plantations ($z = 3.582$, $P < 0.001$).

We did not find significant differences in habitat use of continuous native vegetation and native vegetation remnants (red deer: $z = -1.277$, $P = 0.202$; wild boar: $z = 0.628$, $P = 0.530$; European hare: $z = 1.129$, $P = 0.259$). We also did not detect differences in use

Table 1. Frequency of detections and recording rate of red deer, wild boar and European hare in the different habitat types

		Native vegetation		Pine plantation		
		CNV	NVR	DPP	SPP	Firebreak
Red deer	N° stations with presence	4 (20%)	4 (40%)	15 (75%)	7 (78%)	10 (100%)
	Total records	5	7	68	60	49
	Mean records/10 days (SE)	0.02 (0.01)	0.02 (0.02)	0.28 (0.06)	0.57 (0.22)	0.33 (0.10)
Wild boar	N° stations with presence	6 (30%)	2 (20%)	15 (75%)	8 (89%)	8 (80%)
	Total records	8	2	53	25	32
	Mean records/10 days (SE)	0.03 (0.01)	0.00 (0.00)	0.22 (0.07)	0.37 (0.11)	0.30 (0.11)
European hare	N° stations with presence	6 (30%)	2 (20%)	7 (35%)	4 (44%)	9 (90%)
	Total records	26	3	22	43	100
	Mean records/10 days (SE)	0.11 (0.06)	0.03 (0.03)	0.09 (0.05)	0.40 (0.33)	0.88 (0.20)

CNV, continuous native vegetation; DPP, dense pine plantation; NVR, native vegetation remnants; SPP, sparse pine plantation.

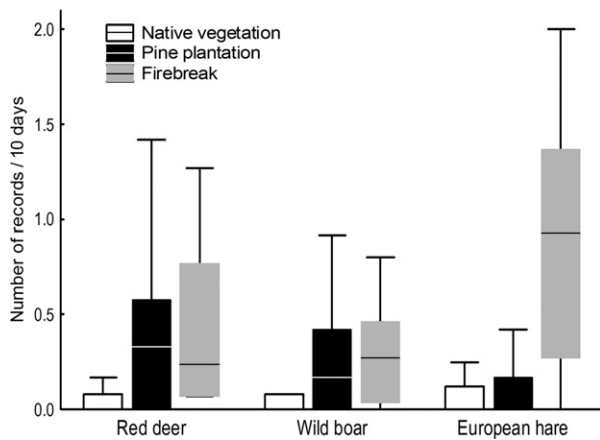


Fig. 1. Box plot of habitat use of the introduced herbivore species in each habitat type, measured as number of records per 10 days. The median is illustrated in the box. The bottom of the box is at the 20% percentile, and the top is at the 80% percentile. The whisker extends to the lowest and highest value in the data.

of dense and sparse pine plantations (red deer: $z = -1.644$, $P = 0.100$; wild boar: $z = -1.102$, $P = 0.271$; European hare: $z = 0.316$, $P = 0.752$), although red deer tended to use sparse pine plantations more frequently (Table 1).

Habitat models

We found no spatial autocorrelation at scales of 1 km or higher, the minimum distance between sampling stations. In logistic models we used five habitat variables for red deer and wild boar, and four for European hare (Tables 2,3). The model with the lowest AIC score for red deer contained two variables, one at the stand scale: mid-storey richness, which was negatively related with its habitat use; and one at the landscape scale: proportion of area covered by pine plantation

Table 2. Habitat variables correlated with the presence of introduced herbivorous mammals, used to perform the habitat models

Variable type	Code	Detail
Stand scale	UndRic	Understorey richness (number of species)
	BarCov	Bare cover (%)
	MidCov	Mid-storey cover (%)
	MidRic	Mid-storey richness (number of species)
Landscape scale	CanCov	Canopy cover (%)
	PrAcSt0.5k	Proportion of area covered by <i>Austrocedrus chilensis</i> forest/steppe within 0.5 km of the sampling station
	PrNa0.5k	Proportion of area covered by <i>Nothofagus antarctica</i> shrubland within 0.5 km of the sampling station
	PrPi0.5k	Proportion of area covered by pine plantation within 0.5 km of the sampling station
	MPSAcSt1k	Mean patch size of <i>A. chilensis</i> forest/steppe within 1 km of the sampling station (ha)
	MPSPi0.5k	Mean patch size of pine plantation within 0.5 km of the sampling station (ha)

within 0.5 km of the sampling station, which was positively related with its habitat use (Table 4). For wild boar, the model with the lowest AIC value included three habitat variables, one at the stand scale: mid-storey cover, negatively related with its habitat use index, and two at the landscape scale: proportion of area covered by *N. antarctica* shrubland within 0.5 km of the sampling station, negatively related with its

Table 3. Summary of variables included in the logistic regression models for each species, and selection estimators for each model

Species	Variables	AIC	Δ AIC	% PCC	% ACC	% OCC
Red deer	PrP10.5k + MidRic	80.11	0	82.50	65.52	75.36
	PrP10.5k + UndRic + MidRic	82	1.89	82.50	65.52	75.36
	PrP10.5k + UndRic + MidRic + PrAcSt0.5k	83.96	3.85	82.50	65.52	75.36
	MidCov + PrP10.5k + UndRic + MidRic + PrAcSt0.5k	85.95	5.84	82.50	65.52	75.36
Wild boar	MidCov + PrNa 0.5k + MPSP10.5k	87.27	0	78.95	64.52	72.46
	MidCov + PrNa0.5k	87.27	0	78.95	54.84	68.12
	MidCov + MidRic + PrNa0.5k + MPSP10.5k	88.08	0.81	84.21	61.29	73.91
	MidCov + MidRic + PrNa0.5k + MPSAcSt1k + MPSP10.5k	90.08	2.81	84.21	61.29	73.91
European hare	MidCov + CanCov	87.92	0	32.00	86.36	66.67
	MidCov + CanCov + PrAcSt0.5k	88.56	0.64	40.00	88.64	71.01
	BarCov + MidCov + CanCov + PrAcSt0.5k	89.84	1.92	40.00	84.09	68.12

For variable definitions, see Table 2. ACC, absences correctly classified; OCC, observed correctly classified; PCC, presences correctly classified.

Table 4. Parameters of the selected logistic regression model for each species

Species	Variables	β	SE	Wald	<i>P</i>	Exp(β)
Red deer	PrP10.5k	2.803	0.927	9.144	0.002	16.495
	MidRic	-0.198	0.092	4.616	0.032	0.820
	Constant	0.065	0.736	0.008	0.929	1.067
Wild boar	MidCov	-0.022	0.016	1.798	0.180	0.979
	PrNa0.5k	-4.779	2.854	2.804	0.094	0.008
	MPSP10.5k	0.045	0.036	1.619	0.203	1.046
	Constant	0.584	0.642	0.827	0.363	1.793
European hare	MidCov	-0.047	0.020	5.394	0.020	0.954
	CanCov	-0.015	0.008	3.802	0.051	0.985
	Constant	0.651	0.510	1.628	0.202	1.917

For variable definitions, refer to Table 2.

habitat use, and mean patch size of pine plantation within 0.5 km of the sampling station, positively related with its habitat use (Table 4). For the European hare, the model with the lowest AIC score included two stand-scale variables: mid-storey cover and canopy cover, both negatively related with its habitat use (Table 4).

DISCUSSION

Our results revealed that red deer and wild boar had a strong preference for pine plantations, and showed associations with cover and size of plantations at the landscape scale and structural characteristics common in pine plantation, such as low mid-storey cover, at the stand scale. These findings are consistent with our hypothesis and with an invasional meltdown effect (Simberloff & Von Holle 1999). In contrast, despite the fact that the European hare is a species associated with open areas, the replacement of native vegetation with pine plantations did not

appear to negatively affect its habitat use. However, this species was favoured by the presence of disturbed areas, such as firebreaks, with low arboreal and mid-storey cover. It must be highlighted that we studied only the nocturnal habitat use of the three species, and although these species are mainly active during dawn and dusk, they could show some activity during the day that was not described in this work (Georgii & Schröder 1983; Graves 1984; Homolka 1986). In this way, interpretation of results must be limited to nocturnal activity.

Red deer have been described as commonly occurring in woodlands with grassy clearings (Mitchell *et al.* 1977), while wild boar prefer broadleaved forests but may occur in more open habitats, such as steppe, shrubland and farmland (Spitz 1999). Our findings suggest that the establishment of pine plantations in native open habitat areas generates an edge habitat of woodland–grassland interface that may offer optimal conditions for these species. Habitat use by both species is strongly shaped by availability of food and shelter against weather and predators (Kurz

& Marchinton 1972; Putman 1988). In this way, forest plantations established in open habitats could provide a greater combination of food and cover, as in general terms, open areas like native vegetation may provide better forage (Nuñez *et al.* 2008; Relva *et al.* 2010) but are more exposed, while closed habitats like pine plantation provide shelter against both climate and predators (Peek *et al.* 1982).

Although use of pine plantations and native vegetation differed significantly, structural differences within vegetation types did not appear to have a significant effect on habitat selection by these species; we did not observe differences in use of small patches and continuous areas of native vegetation or in use dense and sparse plantations. This suggests that habitat selection by those species is shaped by the presence of an overstorey stratum, but not by internal differences in vegetation structure within forested and non-forested habitats. On the other hand, both species made significant use of firebreaks, which could be acting as environments where these species find a greater availability of food, or can move among habitats in search of food and water. European hares, in turn, were much more abundant in firebreaks than in other types of vegetation, suggesting that these treeless strips may also act as habitat for this species.

The spread of red deer and wild boar in Patagonia began less than a century ago, and it has been suggested that the distribution of the species has not reached a state of equilibrium yet (Flueck & Smith-Flueck 1993; Pescador *et al.* 2009). In the Patagonian region, both species first populated the Andean forests and ecotone in the northwest, but recently have begun to expand into steppe habitats (Novaro & Walker 2005; Novillo & Ojeda 2008). In this way, the establishment of conifer plantations in steppe areas near the forest ecotone could be favouring the spread of red deer into the steppe, as suggested by Flueck *et al.* (2003). A similar situation has been documented in the UK, where farm woodlands expanded in open hills (Putman & Moor 1998). In this latter case, it has been suggested that this process has resulted in both increasing deer densities within the original geographical range and providing pathways to new areas by creating more refuges (Putman & Moor 1998).

Plantation forests may negatively impact adjacent natural land cover by increasing abundances of red deer and wild boar, which then spread into neighbouring areas and impact native communities (Vázquez 2002), croplands (Bonino 1995), and young plantations (Bonino 1995). Moreover, the increased abundance of introduced herbivores inside plantations may increase the abundance of native predators. Pine plantations in the region harbour fewer native birds (Lantschner *et al.* 2008; Paritsis & Aizen 2008) and

rodents (Lantschner *et al.* 2011) than do native habitats, and we did not record any native medium or large herbivores inside plantations. Consequently, introduced herbivores may represent an important food supply for native predators, whose diet in the region has been found to be mainly comprised of exotic species (Novaro *et al.* 2000). This pattern may be particularly important for *Puma concolor*, which has been found to positively select pine plantations (Lantschner *et al.* 2012).

In sum, the synergistic effect generated by facilitation between pine plantations and introduced herbivores is likely to have several ecological implications, both for pine plantations and adjacent native environments. Currently, the planted area in the region is relatively low and restricted in distribution, and as a consequence the overall impact is likely to be also correspondingly low. However, potential future increases in the amount of area in plantation forests could have important consequences over broad areas. We suggest that future decisions to convert current patterns of land use should consider their effects on invasive species and consequently should be accompanied by management plans specifically designed for the introduced herbivores.

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