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Native forest replacement by exotic plantations triggers changes in prey selection of mesocarnivores

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ABSTRACT

Replacement of native forests by forest plantations may change the composition and abundance of small mammals, thus influencing the foraging behavior of mesocarnivores in these human-created habitats. We assessed how differences in prey abundance between native forests and exotic plantations in southern Chile may explain the prey selection of four mesocarnivores, as analyzed from their scats. Using a spatial zero-inflated Poisson model, we determined that the abundance of most small mammals was lower in plantations than native forests, except for three common species, which had similar or larger abundances in exotic plantations. We assessed mesocarnivores' prey selection by assessing the coefficients and log-ratios of use and availability of a Bayesian Resource Selection Function. We determined that in native forest, the preferences of kodkod (*Leopardus guigna*) for arboreal prey was stronger, whereas chilla fox (*Pseudalopex griseus*) and Darwin's fox (*Pseudalopex fulvipes*) exhibited a selective preference for ground prey. Darwin's fox also exhibited a habitat-dependent changes in their selection for Darwin's leaf-eared mouse (*Phyllotis darwini*), from a positive log ratio in native forest to a negative ratio in exotic plantations. Conversely, culpeo fox (*Pseudalopex culpaeus*) selected long-tailed colilargo (*Oligoryzomys longicaudatus*) and Chilean climbing mouse (*Irenomys tarsalis*) in plantations only, even though these prey were more abundant in native forests. Although mature commercial forest plantations may provide feeding grounds for mesocarnivores, depending on their species-specific ability to capture available prey, the decline of small mammal availability in plantations may modify the prey selection of mesocarnivores.

1. Introduction

Exotic plantations are becoming increasingly widespread as natural ecosystems are replaced by productive forestry lands (FAO, 2011), thus changing the distribution and abundance of species throughout different trophic levels (Brockerhoff et al., 2008; Lindenmayer and Hobbs, 2004). Carnivores can respond positively, or negatively, to plantations depending on their ecological requirements and management prescriptions within these anthropic habitats (Acosta-Jamett and Simonetti, 2004; Di Bitetti et al., 2006; Pita et al., 2009; Mazzolli, 2010; Lantschner et al., 2012; Simonetti et al., 2013; Coelho et al., 2014). The decline in carnivore populations arising from the replacement, or loss, of natural habitats may result in cascading effects affecting the biodiversity at lower trophic levels (Jaksic et al., 1992, Thompson and Gese, 2007, Byrom et al., 2014; Ripple et al., 2014). Assessing how exotic plantations alter prey populations and how carnivores respond to these habitat-mediated changes in prey abundance could provide a bridge between sustainable forestry management and the trophic ecology of carnivores.

Small mammal species represent a significant amount of animal biomass available for mesocarnivores in natural forest ecosystems (Carey and Johnson, 1995; Hanski et al., 2001; Korpimaki et al., 2005; Dupuy et al., 2009). Although small mammals could be abundant in productive land, such as forest plantations, due to their habitat generalism or large mammal extirpation (e.g., Muñoz-Predreros et al., 1990; Lindenmayer and Hobbs, 2004; Saavedra and Simonetti, 2005; Lantschner et al., 2011; Young et al., 2015), the overall density of small mammals tends to decrease as native habitat is disturbed. Indeed, habitat quality for small mammals decreases by the loss of habitat elements contributing to habitat complexity, such as understory cover, logs, snags and large decayed trees (Lindenmayer et al., 1994; Carey and Johnson, 1995;

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Lindenmayer and Hobbs, 2004; Saavedra and Simonetti, 2005; Robitaille and Linley, 2006; Fontúrbel, 2012). Small mammals living in plantations may not only be limited by food, but also by a reduced availability of natural refuges used against predators (e.g., burrows, tree holes, and cavities; Balme et al., 2007; Gorini et al., 2012; Escobar et al., 2015).

Mesocarnivores inhabiting landscapes dominated by plantations can respond to changes in small mammal composition and abundance by modifying their prey selection patterns. Predators can become more efficient at searching for, pursuing and capturing the more abundant prey species (Emlen, 1966; Murdoch, 1969; Charnov, 1976; Chesson, 1983; Jaksic et al., 1992; Joly and Patterson, 2003; Prugh, 2005; Dell'Arte et al., 2007). However, depending on their species-specific attributes, carnivores' ability to search and find prey could increase in forest plantations with poorly developed vegetation (Mills et al., 2004; Gorini et al., 2012). The sensitivity of carnivores to habitat modifications resulting from forest plantations, may depend on their species-specific habitat specialization, which influences their capacity to adjust foraging behavior in response to changing habitat conditions (Gorini et al., 2012). Therefore, depending on their ability to respond to habitat-dependent changes in prey catchability and abundance, carnivores may modify their prey selection behavior when native habitats are replaced by exotic plantations.

Mesocarnivores occurring in temperate forests of central-south Chile face considerable structural and compositional habitat change resulting from intensive forestry land use (Aguayo et al., 2009). However, recent studies have shown that exotic plantations are not “biological deserts” for these species because they can provide alternative habitats through the maintenance of native understory and landscape heterogeneity (Lindenmayer and Hobbs, 2004; Simonetti et al., 2012; Simonetti et al., 2013). Exotic plantations in this region support fewer small mammals species compared to native forests. In some cases, however, plantations might harbor a high abundance of sigmodontine species, such as long-haired field mouse (*Abrotix longipilis*), olivaceous field mouse (*Abrotrix olivaceus*) and long-tail colilargo (*Oligoryzomys longicaudatus*) (e.g., Muñoz-Pedreros, 1992; Saavedra and Simonetti, 2005; García et al., 2013). Thus, even though the structural role of exotic plantations as habitat for carnivores – and other taxa – has been documented (e.g., Simonetti et al., 2013; Cerda et al., 2015), the functional role of these human-created lands, as feeding grounds for mesocarnivores is poorly understood.

Mesocarnivores living in temperate forest have been shown to prey on a wide range of small mammals species (e.g., Jiménez et al., 1990; Roa and Correa, 2005; Sade et al., 2012). However, carnivores prey use in relation with changes in prey availability arising from the replacement of native forest by plantations is unknown. Addressing this knowledge gap is essential because exotic plantations currently cover almost 17% of forested areas in Chile (CONAF, 2011). In this study, we investigated the role of exotic plantations as feeding grounds for four sympatric native mesocarnivores inhabiting a mosaic landscape dominated by exotic plantations in central-south Chile: kodkod (*Leopardus guigna*), Darwin's fox (*Pseudalopex fulvipes*), culpeo fox (*Pseudalopex culpaeus*) and chilla fox (*Pseudalopex griseus*). The Vulnerable kodkod and the Critically Endangered Darwin's fox (Napolitano et al., 2015; Jiménez et al., 2008, respectively) have been documented to be negatively affected by exotic plantations (Acosta-Jamett and Simonetti, 2004; Moreira-Arce et al., 2015), yet mechanisms underlying their responses remain unclear. Specifically, we assessed variation in the abundance of small mammals between plantations and native forest and we asked whether this prey variation triggered changes of prey selection patterns on these carnivores. First, we predicted that in exotic plantations compared to native forest, the overall abundance of small mammals is lower as previously documented in other studies (e.g., Saavedra and Simonetti, 2005; García et al., 2013). Second, we predicted that these mesocarnivores respond to changes in small mammal abundances by switching their prey selection patterns towards the prey species that are more abundant at each habitat type. However, we predicted that prey selection behavior of forest-specialist kodkod and Darwin's fox may also be affected by changes in habitat structure as derived from replacement of native forest into exotic plantations.

2. Methods

2.1. Study area

The study area encompassed ca. 16,000 ha and is located in Nahuelbuta Mountain Range (NMR), in Temperate Forest of southern Chile (Fig. 1). Climate is characterized by hot, dry summers (mean monthly temperature and rainfall 16.4 °C and 22.5 mm, respectively) and cool, wet winters (monthly means: 7.5 °C and 205.4 mm). The elevation of the study area ranged from 650 to 900 m. Nahuelbuta Mountain was once widely covered by continuous forest composed by mixed deciduous and evergreen species such as *Araucaria araucana*, *Eucryphia cordifolia*, *Aextoxicon punctatum* and *Laureliopsis philippiana* as well as a mixture of *Nothofagus* species (Smith-Ramírez, 2004). Currently, the landscape is a mosaic of human-created lands, composed of a combination of young and mature exotic forest plantation stands of Monterrey pine (*Pinus radiata*) and *Eucalyptus* spp., and remnants of native forest (Fig. 1). Young plantations comprise poorly developed understory, whereas mature exotic plantations are characterized by the presence of a scattered understory vegetation composed by native shrubs (e.g., *Aristotelia chilensis* and *Chusquea quila*), but also by introduced shrubs (e.g., *Rubus ulmifolius*, *Ulex europaeus* and *Teline monspesulana*, see Poch and Simonetti, 2013). Understory vegetation of the native forest includes dead trees and fallen logs, as well as a rich diversity of native shrub species, native tree saplings, mosses, ferns and climbing plants, such as *Azara* spp., *Gevuina avellana*, *Berberis* spp., *Blechnum* spp., *Luma apiculata*, *Myrceugenia exsucca* and *C. quila*.

2.2. Prey abundance

Prey abundance was assessed from relative abundance of prey estimates obtained from small mammal trapping conducted during spring 2012 and autumn of 2013. The abundance of some small mammal species tends to vary markedly from spring to autumn (Murua et al., 1986; Meserve et al., 1991; Meserve et al., 1999); hence, their abundance was assessed in these two seasons. We used a combination of wire-mesh (Tomahawk-like) and Sherman (7.6 × 8.9 × 22.8 cm) traps in 40 grids of 6 × 6 live traps each. Grids were at least 1000 m apart from each other and distributed across two habitat types, with 20 grids located in mixed forest dominated by southern beech (*Nothofagus* spp.), and 20 in monoculture exotic plantations of Monterrey pine (Fig. 1). At each grid, half traps were consistently placed on and above ground level (~2 m height) in order to improve the capture of both ground-level and arboreal small mammals (Fontúrbel et al., 2010). Trapping at each grid was conducted for five consecutive nights (totaling 7200 trap-nights), using rolled oats as bait. Captured individuals were identified to species, marked with unique patterns in their fur, and released at the capture site. Differences in small mammal abundance between native forests and plantations can be masked by the seasonal variations of some rodent species in temperate ecosystems, as explained above. Therefore, we included season as a covariate to account for seasonal fluctuations of abundance (see below).

We used the minimum number of small mammals known alive (MNKA; Lancia et al., 1994) to obtain estimates of absolute and relative small mammal abundances in different seasons and habitats.