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Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: A multi-scale approach

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ABSTRACT

Habitat-specialists have narrower niches, but achieve higher or similar peak performance (e.g. occurrence probability, ψ) than habitat-generalists along resource gradients that may be selected from the stand- to landscape-levels. Understanding the relationship between niche width and ψ of forest owls will facilitate the development of appropriate management recommendations for their conservation. We assessed ψ of the threatened habitat-specialist rufous-legged owls (*Strix rufipes*) and habitat-generalist austral pygmy-owls (*Glaucidium nana*) across three spatial scales, and tested whether they differed in resource utilization and peak ψ in temperate forests of southern Chile. We conducted 1145 broadcast surveys at 101 sites and used multi-season occupancy models, accounting for imperfect detection, to estimate ψ. For *S. rufipes*, ψ ranged between 0.05 and 1 across sites, and was positively associated with the variability (standard deviation, SD) in diameter at breast height (DBH) of trees and bamboo understory density. For *G. nana*, ψ ranged between 0.67 and 0.98, and was positively associated with forest-patch shape index (irregularity and edge effects) and forest cover at 180 ha, although the parameter estimates were imprecise. Relative to *G. nana*, *S. rufipes* had lower total resource utilization due to lower ψ over gradients of all covariates, but achieved similar peak ψ for resources related with stand-level forest complexity and forest stability at the landscape scale. Occurrence of habitat-specialist owls will be promoted if multi-aged stands with a variety of tree sizes (SD of DBH = 19.9 ± 9 cm), including large old-growth trees, with relatively high bamboo cover (34.2 ± 26.6%), are retained. Landscapes with forest cover >63.5% would also favor occurrence by habitat-specialist owls.

1. Introduction

Niche theory has a long history in ecology and it is helpful for assessing the condition of ecological communities (Clavel et al., 2011; Hirzel and Le Lay, 2008). In a niche context, specialist species have a narrower width in resource use than generalists (i.e. generalists utilize a greater variety of resources, Fig. 1a). Nevertheless, specialists can reach either a higher or similar level of peak performance (e.g. occurrence, density) than generalists under a subset of relatively stable resources (Fig. 1b and c; Devictor et al., 2010; Peers et al., 2012). Narrower niches render specialists more prone to be negatively affected by habitat degradation and fragmentation, than generalists (Clavel et al., 2011). Therefore, identifying habitat attributes where specialist species have higher peak performance is essential for the development of management guidelines that conserve a diversity of species within a community.

Owls act as apex predators within forest communities, and the implementation of plans for their conservation may deliver enhanced biodiversity benefits (Sergio et al., 2006). To meet their niche requirements, forest owls usually require different habitat patches for breeding and foraging, and thus they select habitat resources from the stand- to the landscape-level (Flesch and Steidl, 2010). Therefore, multi-scale approaches can be useful to identify: (a) relevant scales concerning individual perception of the environment so as to generate habitat suitability models (Martínez et al., 2003; Sergio et al., 2003), and (b) the level of

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sensitivity of species in habitats subject to rapid degradation and fragmentation.

South America hosts the southernmost temperate forests in the world (Armesto et al., 1998). These ecosystems are recognized as a biodiversity "hotspot" because of their high concentration of endemic species, and are subject to conservation concern due to high rates of anthropogenic degradation and fragmentation (Myers et al., 2000). Here, intensive land-use practices have degraded stand-level availability of structural attributes such as the volume of coarse woody debris, large decaying trees and understory vegetation, and thus wildlife populations depending on these niche resources have been negatively affected (Díaz et al., 2005; Reid et al., 2004). At the landscape scale, southern temperate ecosystems have been reduced and fragmented, converting continuous forest into a patchwork of habitat types (Echeverría et al., 2006).

Habitat suitability models offer an operational application of the ecological niche as they presuppose that the observed occurrence of an owl at a site reflects its ecological requirements (Hirzel and Le Lay, 2008). However, the relation between niche requirements and the occurrence patterns of forest owls may sometimes be equivocal as these birds are elusive and mainly nocturnal, and therefore a non-detection of individuals at a site does not mean the species is absent. With the exception of Sberze et al. (2010), most studies on raptor-habitat relations in South America have made the assumption that owl detectability was perfect. This assumption may underestimate the number of sites where owls achieve their niche requirements and miss relevant habitat resources (MacKenzie et al., 2003).

One way to compare niches is to develop habitat models of sympatric species independently and contrast their characteristics (Hirzel and Le Lay, 2008). We studied two sympatric owls that hypothetically differ in site-occurrence patterns and sensitivity to forest degradation and fragmentation: rufous-legged owls (*Strix rufipes*) and austral pygmy-owls (*Glaucidium nana*). Both species occur extensively across South American temperate forests (35–55°S). *S. rufipes* are one of the least known owls in South America with suspected declining populations due to native forest loss (Martínez and Jaksic, 1996). *G. nana* are the most widespread and common owls in Chile (Jiménez and Jaksic, 1989). Previous research suggests that *S. rufipes* inhabit a more specific range of stand-level habitat resources than *G. nana* (Ibarra et al., 2012). *S. rufipes* are considered habitat-specialists because of their affiliation with multi-stratified forest stands >100 years old, whereas *G. nana* are considered habitat-generalists as they utilize a range of environments including forests, forest-steppe ecotones, shrublands and occasionally urban parks (Jiménez and Jaksic, 1989; Martínez and Jaksic, 1996; Trejo et al., 2006). However, whether these species actually differ in either occurrence rates or levels of habitat-specialization have not been tested.

The aims of this study were to (1) examine the association between habitat resources and occurrence patterns for each of these two sympatric forest owls at three spatial scales, and (2) test if habitat-specialist and generalist owls differ in their total resource utilization and peak performance in Andean temperate forests of southern Chile. We predicted that (1) owl occurrence rates are influenced from local within-stand to landscape level habitat resources, and (2) *S. rufipes* have a lower total resource utilization (Fig. 1a) but either a higher (Fig. 1b) or similar (Fig. 1c) level of peak performance for particular niche resources, than *G. nana*. To examine owl occurrence patterns and test our predictions, we used occupancy models that account for the likelihood that owls occurred at some sites without detections (i.e., were present but not detected, Ibarra et al., 2014). Our models allowed us to identify key niche resources to which owls are associated, and thus can provide reliable recommendations for owl conservation.

2. Materials and methods

2.1. Study area

The 2585 km^2 study area lies within the Villarrica watershed (39°16′S71°W), located in the Araucarias Biosphere Reserve, southern Chile. We chose this watershed because its rural road and trail system is extensive and accessible, and its landscapes are representative of the Andean portion of Chile's temperate forests (Ibarra et al., 2014). The temperate climate has a short dry season

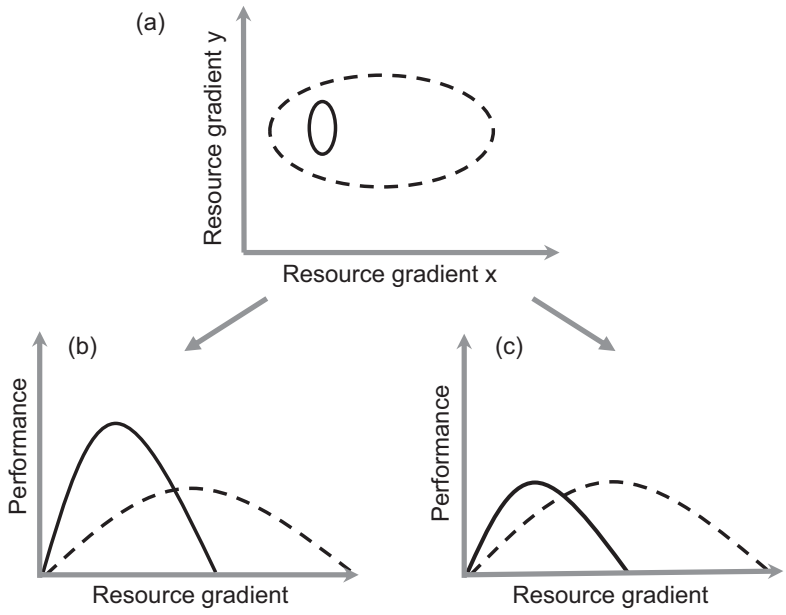

Fig. 1. (a) Specialized species (continuous line) have smaller niche widths than generalized species (dashed line) across resource gradients. Specialists can reach either a (b) higher level of performance (i.e. traditional model of relative niche width between specialists and generalists) or (c) similar level of performance (i.e. alternative model of relative niche width) than generalists, under a subset of resources that are relatively stable.