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Original Investigation

Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations

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ABSTRACT

Small mammals comprise an important component of forest vertebrate communities. Our understanding of how small mammals use forested habitat has relied heavily on studies in forest systems not naturally prone to frequent disturbances. Small mammal populations that evolved in frequent-fire forests, however, may be less restricted to specific habitat conditions due to the instability of these resources in time and space. We investigate how canopy cover and the volume of coarse woody debris (CWD), covariates that are considered important for small mammals, impact abundance and body mass of eight small mammal species. Based on live-trapping data collected across 23 sites over three years in a frequent fire forest in the Sierra Nevada we apply capture-recapture models for stratified populations, a statistically rigorous, rarely used framework that allows joint modeling of detection, abundance and its response to covariates. Canopy cover had a strong negative association with the abundance of yellow-pine chipmunks and California ground squirrels, and a strong positive association with deer mice. CWD had a strong negative association with the abundance of golden-mantled ground squirrels, yellow-pine and long-eared chipmunks, and a strong positive association with deer mice. Whereas canopy cover influenced abundance and body mass similarly, CWD had a positive association with body mass and a negative association with abundance in some species. These patterns could arise if suitable habitat is monopolized by socially dominant individuals. Despite these habitat associations, the small mammal community in our study was dynamic and diverse, with spatial and temporal variation in dominant species suggesting that species were flexible in their use of habitat. This study suggests that it is important to understand the disturbance regimes when investigating habitat requirements, coexistence and evolutionary ecology of small mammal species.

Introduction

Small mammals comprise an important component of the vertebrate biomass and diversity in coniferous forests (Lawlor, 2003). They influence forest vegetation structure through dispersal of seeds and hypogenous fungi (Carey et al., 1999; Price and Jenkins, 1987; Pyare and Longland, 2001) and are an important food source for forest carnivores (Smith et al., 1999; Zielinski et al., 1999). The impact of forest management practices has dominated the ecological context of studies on forest-dwelling small mammals (Bagne and Finch, 2010; Greenberg et al., 2006; Monroe and Converse, 2006). One overriding theme of these studies is that human-induced disturbance to these systems has led to a decrease in old-growth forest specialists such as voles and northern flying squirrel (Carey and Johnson, 1995; Fauteux et al., 2013; Lemaître et al., 2010; Smith, 2007). Whereas specialists are expected to evolve in relatively stable or homogeneous environments, niche theory predicts that heterogeneous environments or environments with frequent disturbances will be dominated by generalists (Devictor et al., 2008; Kassen, 2002).

The coniferous forests of the western United States were historically exposed to regular fires. A century of fire suppression, in combination with intensive timber harvest, has drastically altered forest structure and disturbance regime. Where large overstory trees were removed during early timber harvests, subsequent fire

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suppression has resulted in relatively homogeneous, even-aged forest stands with denser canopies (Knapp et al., 2013). Compared to more mesic forests, studies of small mammals in high-frequency fire forests are few and have been largely restricted to the more homogeneous forests of the interior US (Stephens et al., 2012, 2014). In addition, because these studies were usually conducted shortly after mechanical thinning or prescribed fire, it has been difficult to ascertain whether wildlife responses are a consequence of disturbance or changed habitat structure. Therefore, the spatial and ecological context of previous studies limits inferences about habitat associations and the impact of forest management on small mammals that evolved in forests with frequent disturbance regimes.

The presence and abundance of small mammals in forested habitats is often correlated with habitat structure (Hallett et al., 2003; Johnston and Anthony, 2008; Lawlor, 2003; Naxara et al., 2009). Canopy cover, for example, influences the availability of resources on the forest floor, and small mammals are frequently positively associated with more open forests (e.g., Bellows et al., 2001; Greenberg et al., 2006), which are characterized by denser, more complex understory vegetation (Knapp et al., 2013). Downed coarse woody debris (CWD) is also an important habitat feature, as it supports insects and fungi and provides nesting habitat and cover from predators (e.g., Ecke et al., 2002; Fauteux et al., 2013, 2012; Hinkelman and Loeb, 2007; Vanderwel et al., 2010).

Habitat associations of small mammals are most frequently assessed using abundance estimates or indices thereof (e.g., Converse et al., 2006; Coppeto et al., 2006; Fauteux et al., 2012). Several studies, however, have argued that abundance alone is not necessarily a good proxy for habitat quality (e.g., Battin, 2004; Robertson and Hutto, 2006; Van Horne, 1983). Areas with high abundance can consist of suboptimal or even sink habitats, harboring the “spillover” from high quality, or source habitat. Often, these sinks harbor competitively inferior individuals that are unable to establish themselves in high quality patches (Ecke et al., 2002; Van Horne, 1983). To disentangle the effects of habitat quality and competition, it is important to look at abundance in combination with indicators of physical condition of animals, such as their body mass (Greenberg et al., 2006).

Live trapping is a standard tool in the study of small mammal populations. Although the importance of accounting for imperfect and varying detection probability in the study of animal populations has long been recognized (e.g., Nichols, 1992; Otis et al., 1978), many contemporary small mammal studies still ignore detection bias and draw inference on raw counts (e.g., Amacher et al., 2008; Bellows et al., 2001; Coppeto et al., 2006; Fauteux et al., 2012; Kelt et al., 2013; Lee et al., 2008). When combined with capture-recapture modeling, however, live trapping studies can produce unbiased estimates of abundance while accounting for imperfect detection probability (e.g., Converse et al., 2006; Monroe and Converse, 2006). If applied at various sites, estimates can be related to site-level covariates. Until recently, such analyses have mostly been applied post hoc (Converse et al., 2006), or directly to uncorrected numbers of individuals captured (see above). The latter approach fails to account for detection probability, and thus carries an inherent risk of bias, especially when detection varies by species or with covariates that are considered to influence abundance (e.g., Monroe and Converse, 2006). Post hoc regression of abundance estimates against predictor variables is complicated because uncertainty of the estimates, which is bound to vary in its magnitude across estimates, has to be taken into account (Converse et al., 2006). Recent model developments allow for the joint estimation of abundance and its response to covariates across multiple sites (or otherwise defined groups) in a unified capture-recapture framework for stratified populations (Converse and Royle, 2012; Royle et al., 2014). The approach accounts for imperfect detection, and allows modeling of population level response to explanatory covariates, while fully accounting for uncertainty on all levels of the model. Although this conceptually coherent analytical framework accommodates a data structure that is common in the study of small mammals, it remains infrequently used.

Here, we use capture-recapture (CR) models for stratified populations to investigate the response of the small mammal community to habitat features that have been altered by recent forestry practices. Our study spans three years of live trapping data collected across 23 sites in the Lake Tahoe Basin of the Sierra Nevada, which was heavily logged during the mid-19th century. We investigate how forest structure impacts the abundance and physical condition of 8 small mammal species associated with these traditionally frequent-disturbance forests. Based on the available literature, we predict that higher levels of coarse woody debris and lower levels of canopy cover will positively affect small mammal abundance and physical condition. The results of this study contribute to our understanding of how small mammal communities that evolved under a frequent fire regime are shaped by forest structure and by competition.

Material and methods

Study site

We used live-trapping data from 23 sites in the upland forests of the Lake Tahoe Basin, straddling the states of California and Nevada, USA, in the central Sierra Nevada. The basin lies in a transition zone between Mediterranean and continental climates, creating a great diversity of habitats and leading to the juxtaposition of habitat for several small mammal species. Prior to Euro-American influence, the basin experienced fires every 3–4 years with site fire return intervals of every 8–17 years. A century of fire suppression, intensive logging, and urbanization has resulted in homogenization of the basin’s landscapes and coarse scale heterogeneity (Beaty and Taylor, 2008). Our study sites were located in the lower montane zone at altitudes of 1900–2250 m, and dominated by Jeffrey pine (*Pinus jeffreyi*) forest, white fir (*Abies concolor*) forest, and mixed-conifer forest (Jeffrey pine, white fir, incense cedar *Calocedrus decurrens*, sugar pine *P. lambertiana*, and red fir *A. magnifica*).

Small mammal trapping

At each site, we established one trapping grid that was sampled in two of three consecutive years (13 sites in 2009/2010, 10 sites 2010/2011), resulting in 46 site-year combinations, which constitute the sampling groups. Each trapping grid consisted of 72 (2009), 54 (2010) and 48 (2011) trap stations (reduced over time due to logistical constraints) with a 30-m spacing between stations. This design represents a balance between covering a sufficient number of home ranges of the larger squirrels and obtaining a high enough recapture rate for the smaller species to obtain reliable estimates of density (Converse et al., 2006). At each station we set one Tomahawk trap ($12 \times 12 \times 40$ cm) and one extra-large Sherman trap ($10 \times 11 \times 38$ cm). Tomahawk traps were attached to trees >20 in diameter at breast height, 1.5–2.0 m above ground, and wrapped in a polytarp for cover. Sherman traps were placed at the base of trees, along larger logs or under shrubs, covered with natural materials to insulate them from sun and rain, and with polystyrene in the back to provide further insulation. We baited all traps with a mixture of oats, peanut butter, raisins, and molasses. We pre-baited traps for 3–4 days and subsequently opened traps for a single 4.5-day trapping period, checking traps in the morning and evening. With the exception of shrews, all individuals were marked with uniquely numbered ear tags (model 1005-1). We recorded the species, age,