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Bayesian models describing microhabitat associations of infrequently captured small mammals sampled under a complex hierarchical design

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ABSTRACT

Knowledge about the relationship between habitat structure and abundance of a target species facilitates biodiversity conservation in managed forests. However, modeling the relationship for infrequent small mammal species in silvicultural experiments introduces the challenge of excessive zero counts and complex hierarchical sampling. A common solution has been to ignore infrequent species. The goal of this study was to model microhabitat associations of infrequently captured forest floor small mammal species with Bayesian models that accounted for subsampling and the blocking design of a large-scale variable-retention harvest experiment. Poisson, negative binomial and overdispersed Poisson Generalized Linear Mixed Models (GLMMs) were fitted to data for three small mammal species with different rates of capture. Shrew–mole (*Neurotrichus gibbsii*) and Keen's deer mouse (*Peromyscus keeni*) were the two infrequent species and southern red-backed vole (*Myodes gapperi*) was the frequent species selected for modeling. Capture rate was predicted from variables representing vegetation structure, and results were compared to corresponding Generalized Linear Models (GLMs). GLMMs predicted stronger and sometimes contrary effects of vegetation structure with wider confidence intervals compared to GLMs. The overdispersed Poisson GLMM provided the most consistent and adequate fit to infrequent species. Capture rate of the shrew–mole was found to be negatively associated with tall shrub cover and coarse woody debris volume. Similarly, capture rate of Keen's deer mouse was negatively associated with herb cover and coarse woody debris volume. Finally, captures of southern red-backed vole was associated negatively with herb cover and coarse woody debris volume but positively associated with vertical complexity of overstory vegetation. With correct GLMM specification, statistical inferences of habitat predictors were more reliable as autocorrelation between samples was properly accounted for and valid standard errors were estimated. Furthermore, the GLMMs in this study fitted capture rates of infrequent species well and produced admissible results on the association of these species to microhabitat features. Infrequent species need not be excluded from analysis; in fact, inclusion of these species is crucial to conservation of species diversity by designing silvicultural treatments that produce or protect suitable habitat.

1. Introduction

Modeling the relationship between habitat features and species presence or abundance provides the fundamental ecological understanding required for maintaining the biodiversity of managed forests. Beyond gaining ecological insights, the developed relationship can also be used to predict distribution of species across a landscape (Elith and Leathwick, 2009). However, this modeling effort faces two common challenges with data from large-scale silvicultural experiments: (1) a majority of species are captured infrequently and (2) sampling is typically systematic and involves a hierarchical structure.

The first challenge comes naturally from low population abundance and corresponding low detection probability of certain species (Cunningham and Lindenmayer, 2005). A common approach to addressing low abundance and capture frequency has been to exclude infrequently captured species from statistical analysis. Among 23 studies investigating forest floor small mammal responses to silvicultural treatments in the Pacific Northwest, on average only 62% of the captured species were analyzed (e.g., Klenner and Sullivan, 2003; Suzuki and Hayes, 2003). Some species were ignored because they were non-target species or transient species not normally associated with the sampled habitat (Carey and Johnson, 1995), but most were avoided because their low frequency rendered traditional statistical models based on the normal

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distribution unsuitable. One solution has been to group infrequently captured species during analysis (e.g., MacCracken, 2005). Nevertheless, rare species are particularly deserving of conservation efforts because they are most prone to local extirpation (Meffe and Carroll, 1997). For that reason, understanding their individual habitat requirements is crucial to conservation of biodiversity.

The second challenge mentioned above is an unavoidable consequence of field experiments that strive for operational and ecological relevance (Maguire et al., 2007). These experiments generally contain large experimental units that necessitate nested and systematically arranged sampling units, causing observations in an experimental unit to be autocorrelated. To handle potential autocorrelation between subsamples within experiment units, count data from the sampling units are often summarized by experimental unit as a mean or total before analysis (e.g., Steventon et al., 1998). This approach is appropriate if the objective is to assess only stand-level treatment effects. An analysis on the experimental unit level addresses one spatial scale, but it may not be the most efficient use of information contained in individual sampling units. With data aggregation, resolution is lost for detecting microhabitat attributes that drive responses to treatments. For example, Miller and Getz (1973) found that microclimatic conditions likely influenced the local distribution of southern red-backed vole. Thus, greater ecological insight may be gained from statistical models that maintain attributes of sampling units while accounting for dependencies between these units and avoiding data aggregation at the level of entire experimental units.

Variable-retention regeneration harvesting systems are considered preferred options for managing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests on public lands in the Pacific Northwest, USA, where management objectives call for a combination of timber production and other ecosystem services. The resulting complex stand structures are viewed as more amenable to conservation of biodiversity. The systems have specific goals of providing refugia to closed-canopy organisms and promoting more rapid recolonization of regenerated stands by these species (Franklin et al., 1997). To establish successful refugia, knowledge about the habitat elements perceived by targeted taxa and the spatial scale at which they respond are essential. This information can be gained from modeling microhabitat association of targeted taxa.

Forest floor small mammals in the Pacific Northwest forests play an important role as predators, consumers, and prey (Sullivan and Sullivan, 2001), so they contribute to both species and functional diversity of forests (Carey and Johnson, 1995). Individual species are variably associated with coarse woody debris, herbaceous vegetation and fungal fruiting bodies (Ure and Maser, 1982). These habitat variables indicate quantity and quality of cover and food provided by vegetation comprising a forest stand. By knowing the functional associations, silviculturists can design treatments that produce or protect specific habitat structures. Rigorous modeling of habitat associations becomes a key tool of forest management to successfully balance timber harvest with maintenance of forest biodiversity.

The goal of this study was to model the association between microhabitat features and captures of infrequent small mammal species by taking full account of the complex hierarchical design in a large-scale silvicultural experiment in the Pacific Northwest, USA. Three forest floor small mammal species were selected to compare the performance of alternative statistical models for describing the relationship between microhabitat features and capture frequency. Two species were infrequently captured, to the extent that many observations were zero, and one species was very common, resulting in very few zero observations. The statistical models were constructed as Generalized Linear Mixed Models (GLMMs) to accommodate both the nature of count data and the complex hierarchical sampling. Counterparts that ignored the hierarchical sampling structure were formulated as Generalized Linear Models (GLMs) to provide a basis of comparison. The objectives were: (1) to compare modeling results between statistical models that accounted for autocorrelation among sampling units within an experimental unit to those that did not and (2) to provide an example of how these models can enhance knowledge about microhabitat relationships of small mammal species infrequently captured on the forest floor.

2. Materials and methods

2.1. Materials

The Demonstration of Ecosystem Management Options (DEMO) experiment was established as a large-scale operational experiment to assess long-term effects of variable-retention systems on plants, animals, ecological processes and public perceptions in Douglas-fir forests of western Oregon and Washington, USA (Aubry et al., 1999). The silvicultural experiment was implemented under a Randomized Complete Block Design (RCBD) with subsampling. In each of six blocks, two in Oregon and four in Washington (Fig. 1), six 13-ha experimental units were established and treatments were randomly assigned. The six harvest treatments were defined by level (percentage of basal area) and spatial pattern (dispersed vs. aggregated) of retained trees as follows (Fig. 1): (1) 100% retention (100%); (2) 75% aggregated retention (75%A); (3) 40% dispersed retention (40%D); (4) 40% aggregated retention (40%A); (5) 15% dispersed retention (15%D); and (6) 15% aggregated retention (15%A). Halpern et al. (2005) have provided further details on the study sites and vegetation sampling.

In each 13-ha unit, a permanent 8×8 or 7×9 sampling grid with 40-m spacing was installed for vegetation and forest floor small mammal sampling. The grid was buffered by 40 m between the outer grid points and the edge of the unit. At each sample point, small mammals were trapped using a pitfall trap made from two stacked No. 10 cans and operated as a death trap partially filled with water (Gitzen et al., 2007; Oregon Department of Fish and Wildlife Scientific Taking Permits 306-93, 097-34, 075-95, 106-96, 022-99, and 083-00; Washington Department of Fish and Wildlife Permits 99-281 and 00-148). Traps were continuously opened for 28 days between late September and early November, and captured animals were collected and identified weekly (Gitzen et al., 2007). Overstory and understory vegetation were studied concurrently with small mammal trapping. At each sample point, percent cover of herbaceous and small shrub species (<1 m tall) was recorded on a cluster of 24 microplots (0.2×0.5 m). Percent cover of tall shrub species (>1 m tall) and of understory coniferous trees (<5 cm dbh) was measured on four 6-m planar intercepts radiating out from the sample point. Diameter of any downed wood (stems $\geqslant$ 10 cm) was measured at the point of intersection with the vertical plane along these transects. Overstory trees were sampled with nested circular plots that included a 0.01-ha plot for trees with dbh $\geqslant$ 5 and <15 cm and a 0.04-ha plot for trees with dbh $\geqslant$ 15 cm.

At each sample point, the response variable was the total number of captured individuals of a small mammal species. The predictors included six attributes describing vegetation structure at the level of each sample point: (1) mean percent herbaceous cover (HERB,%), (2) mean percent understory conifer cover (CONIF,%), (3) mean percent tall shrub cover (SHRUB,%), (4) mean coarse woody debris volume per hectare (CWDVOL, m^3/ha), (5) overstory crown structural heterogeneity (SHANNON), and (6) stand density (TPH, trees/100-ha). Minima, means, maxima, and standard deviations were summarized in Supporting information (Table S1).

The coarse woody debris volume per hectare was estimated by the conventional technique of planar intersect sampling (de Vries,