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Response of an ecological indicator to landscape composition and structure: Implications for functional units of temperate rainforest ecosystems

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ABSTRACT

We evaluated the northern flying squirrel (*Glaucomys sabrinus griseifrons*), a known associate of key habitat features and processes of old-growth forest, for its capacity as a broad-scale ecological indicator of temperate rainforest ecosystem condition in southeastern Alaska, USA. We utilized a spatially explicit, resource-selection function to evaluate its distribution relative to landscape composition and structure at local (within home-range) and broad (home-range selection) spatial scales, followed by a moving-window analysis to model patch occupancy across this landscape. We found strong support for the influence of type, size, and compositional elements: large, old-growth patches were selected at both spatial scales, and regenerating forest patches ≤40 yrs old were selected against at the broader scale. More importantly, we found that occupancy was related to critical thresholds in composition: patches required ≥73% old-growth forest cover or a minimum total area of 73 ha of old-growth forest to be occupied by flying squirrels. A non-uniform pattern of selection for patches with higher structural connectivity at the local scale, but not at the broader scale, was likely a result of the "empty forest" phenomenon, in which remnant patches were inaccessible in this fragmented landscape. These results are consistent with recent studies of this and related species and suggest that occurrence of northern flying squirrels in southeastern Alaska is influenced by a number of landscape structure and compositional variables that relate critically to late-seral forest conditions. These findings shed new light on the utility of this species as an ecological indicator and its functional relevance to the resilience of fragmented forest ecosystems.

1. Introduction

Ecosystem management has been adopted by many land management agencies as a promising strategy for conserving biodiversity (Christensen et al., 1996), but its application has many practical challenges (Hanley et al., 2005). For example, ecological processes essential for ecosystem function are generally complex and difficult to measure (Meyer and Swank, 1996). Consequently, a common evaluation method has been to monitor indicator species whose biological requirements (e.g., life history or distribution needs) are thought to be dependent on key attributes of a healthy ecosystem (Lindenmayer, 1999). For this strategy to be defensible, however, it is important to test assumptions about species as good indicators of ecosystem condition and to determine thresholds in ecosystem change that yield measurable responses in biological parameters of an indicator species (Dale and Beyeler, 2001; Lindenmayer et al., 2000; Noss, 1999). Furthermore, because ecosystem processes and land management practices operate at variable scales, evaluating those responses at multiple spatial scales helps ascertain the utility of an indicator species (Rondinini and Boitani, 2002).

In managed forests of western North America, the northern flying squirrel (*Glaucomys sabrinus*) has been referred to as a possible indicator species for ecosystem-management (Carey and Johnson, 1995). Although it is not an old-growth forest obligate throughout its range (Smith, 2007), its occurrence, abundance, and reproductive success are associated with microhabitat features of structurally complex, late-seral forests, such as large-diameter trees, snags, a multistory forest canopy, and herbaceous understory cover (Carey, 1995; Holloway and Smith, 2011; Pyare and Longland, 2002; Smith et al., 2004). Furthermore, its movement (i.e., through gliding) is associated with gap dynamics in old-growth forest (Carey, 2000; Scheibe et al., 2007). And finally, its microhabitat use is influenced by the patchy distribution of ectomycorrhizal fruiting bodies that are more abundant in late seral forests (Carey, 2000; Flaherty et al., 2010; Pyare and Longland, 2002; Waters and Zabel, 1995).

These associations collectively suggest that the northern flying squirrel has utility at a broader scale for forest ecosystem

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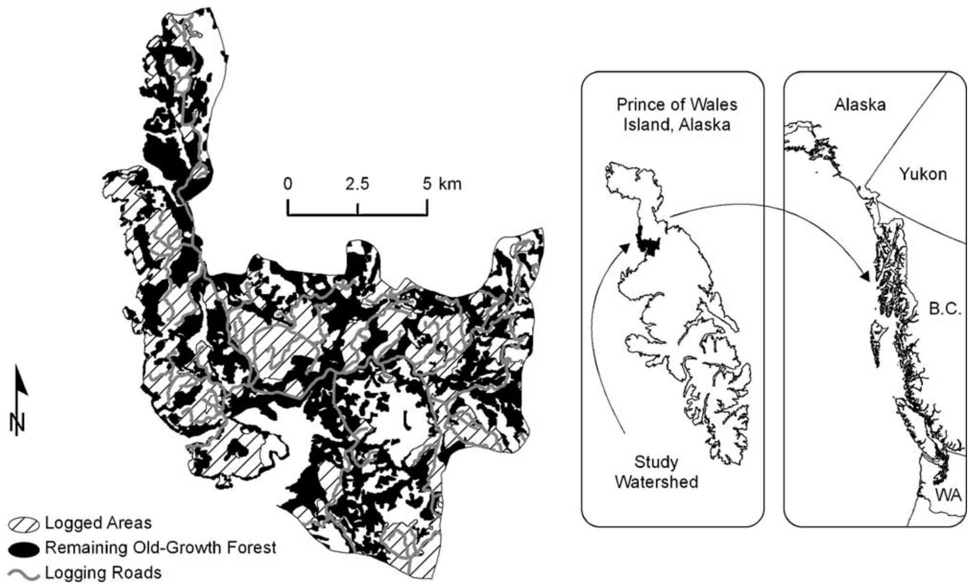

Fig. 1. The extent of the study area watershed (13,020 ha) with a historical logging matrix and remnant old-growth forest fragments, Prince of Wales Island, AK, USA.

management. Its occurrence in individual forest patches is potentially indicative of functionally important attributes of forest health and complexity. Therefore, the compositional and structural requirements for patch-occupancy by the northern flying squirrel are useful guidelines for maintaining ecological integrity across forested landscapes managed for multiple use. For example, the regional persistence and abundance of a related species, the Siberian flying squirrel (*Pteromys volans*), is closely tied to patch occupancy patterns that are influenced by thresholds in the composition, size, and structural connectivity of individual patches (Hurme et al., 2007; Mönkkönen et al., 1997; Reunanen et al., 2004; Selonen et al., 2001; Selonen and Hanski, 2003). Consequently, the Siberian flying squirrel functions as an important indicator in conservation and restoration planning of Eurasian coniferous forest ecosystems (Hurme et al., 2008; Vierikko et al., 2010).

Aspects of the spatial ecology of the northern flying squirrel have received more attention recently (Holloway and Malcolm, 2007; Patterson and Malcolm, 2010; Pyare et al., 2010; Ritchie et al., 2009; Smith, 2012; Smith et al., 2011; Wheatley et al., 2005), but our understanding of patch-occupancy requirements and landscape-level distribution patterns is still inadequate to make informed decisions about conservation and management measures in North American forests. In this study, we evaluated the efficacy of the northern flying squirrel as a broad-scale ecological indicator by studying its distribution relative to landscape structure and composition at multiple spatial scales. We tested hypotheses that the northern flying squirrel would exhibit the following patch-selection patterns: (1) type: selection for old-growth forest fragments and against younger forest and clearcuts (Holloway and Smith, 2011); (2) size: selection for larger old-growth forest fragments (Smith and Person, 2007); (3) composition: selection for greater extent of old-growth forest (Pyare et al., 2010); and (4) configuration: selection for fragments with greater connectivity (Smith et al., 2011).

2. Methods

2.1. Study area

Our study was conducted in the Tongass National Forest, a temperate rainforest in southeastern Alaska, USA (Fig. 1). A dynamic geologic history has created a naturally fragmented island archipelago with a high degree of mammalian endemism (Cook et al., 2006). The maritime climate ranges from the mean daily ambient temperature of 13 °C in July to 1 °C in January and receives 2000–6000 mm of rain annually. There are forests distributed throughout the islands and along the coastal mainland up to approximately 600 m above sea level (Alaback, 1982), with Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and to a lesser extent red-cedar (*Thuja plicata*), yellow-cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), and shore pine (*Pinus contorta*). Since the early to mid-20th century, this landscape has become more fragmented due to extensive clearcut logging, with up to 50% of old-growth forest at low elevations having been harvested on some islands (USFS, 1997). We conducted our study on Prince of Wales Island, which is both the largest island in the Alexander Archipelago and the landscape with the most continuous old-growth logging history. We selected Naukati Creek watershed (13,020 ha) on northern Prince of Wales Island for analysis because it was composed of a matrix of remnant old-growth forest fragments and regenerating clearcuts (Fig. 1) spanning from the 1930s to the present (Fig. 2).

2.2. Animal location data

We established 3 trapping grids to live-capture and radio-collar flying squirrels in remnant old-growth forest fragments. Pyare et al. (2010) provide details on trapping design and we utilized Smith and Nichols' (2003) methodology for live-trapping, handling, and processing of flying squirrels. Adult and juvenile males and females were fitted with 3.0 g radio-transmitters (Model PD-2C; Holohil Systems, Carp, Ontario, CA; 16-week life span). We relocated each animal ≥1 time(s) diurnally and nocturnally each week, until the transmitter signal was no longer detectable. We found diurnal den-tree locations by telemetry-tracking to individual den-trees (Pyare et al., 2010). Locations of nocturnal activities were bi-angulated with two fixed observers. We used the software Location of a Signal (LOAS 4.0; Ecological Software Solutions, LLC) to calculate bi-angulations and evaluate their accuracy. We conducted a series of 64 bi-angulation test-trials with dummy-collars placed in 10 different sites with 9 different observers, and yielded an average bi-angulation accuracy of 139.6 m (SE = 16.6 m). We included only data from individual squirrels with ≥15 locations (Thomas and Taylor, 2006). We used a resulting sample size of 30 individual squirrels