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Using metapopulation models to assess species conservation–ecosystem restoration trade-offs

Connor M. Wood[a,*], Sheila A. Whitmore[a], R.J. Gutiérrez[a], Sarah C. Sawyer[b], John J. Keane[c], M. Zachariah Peery[a]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI, USA
[b] U.S. Forest Service, Pacific Southwest Region, Vallejo, CA, USA
[c] U.S. Forest Service, Pacific Southwest Research Station, Davis, CA, USA

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ABSTRACT

Ecological restoration is needed to counter global-scale ecosystem degradation, but can conflict with endangered species conservation when restoration impacts habitat quality. In such cases, prioritizing long-vacant patches for restoration is an intuitively appealing strategy for minimizing the effects on endangered species. Metapopulation models grounded in empirical data potentially provide a rigorous framework for developing theoretical "patch vacancy thresholds" (i.e., duration of vacancy required before implementing restoration) and assessing the implications of such criteria for restoration objectives. We develop such a model for spotted owls (*Strix occidentalis*), which embody the species–ecosystem dilemma given their preference for closed-canopy forests that are also susceptible to severe fire and drought and hence the center of debates about forest restoration intended to reduce fire and drought risk. We leveraged a > 20-year territory occupancy dataset to parameterize a Stochastic Patch Occupancy Model (SPOM) to assess relative risk to a metapopulation of owls in California under alternative conservation guidelines, including a range of vacancy thresholds. Territories with greater amounts of owl habitat were more likely to be recolonized and less likely to go extinct. Importantly, the probability of a vacant owl territory becoming recolonized declined as length of vacancy increased; territories vacant for 1 and 10 years had annual recolonization probabilities of 0.34 and 0.06, respectively. Based on our SPOM, projected territory occupancy rates declined as the vacancy threshold decreased and as habitat within territories was impacted by restoration. However, more liberal territory vacancy thresholds were projected to increase the proportion of territories (and thus landscape) that could be restored and that restored conditions could be maintained with repeated treatments. Reintroducing natural disturbance regimes, which eliminated the need for repeated treatments, was projected to reduce risk to owls, particularly with relaxed vacancy thresholds. We provide a simple, yet novel, metapopulation framework for quantifying how alternative conservation guidelines might impact owl occupancy and influence forest restoration guidelines. Similar analyses could facilitate restoration efforts in other systems by more explicitly quantifying tradeoffs between species–ecosystem objectives.

1. Introduction

Human activities have resulted in both biodiversity loss and ecosystem degradation worldwide (Barnosky et al., 2011; Vitousek et al., 1997). Consequently, endangered species conservation and ecosystem restoration have emerged as two important paradigms in natural resource management (Groom et al., 2005). Considerable synergy exists between the two paradigms because habitat restoration has improved the status of many threatened or endangered species (Hogg et al., 2013; Lawson et al., 2014; Rannap et al., 2009; Rinkevich, 2005; Webb and Shine, 2000). However, the trade-offs between species conservation and ecosystem restoration (hereafter species–ecosystem) objectives are increasing in this era of global change (Fraser et al., 2017; Peery et al., 2017). Even when endangered species are expected to benefit from restored ecosystems, restoration practices can produce short-term costs to habitat quality that increases extinction risk before predicted benefits of restoration accrue (Warchola et al., 2018). Therefore, uncertainty exists between the potential short-term costs and long-term benefits of restoration for many species such as prairie and forest birds (Powell, 2008; Wilson et al., 1995), grassland insects (Thomas et al., 1986; Warchola et al., 2018), forest reptiles and marsupials (Cunningham et al., 2007), and freshwater fish (Lintermans, 2000). In such cases,

* Corresponding author at: A223 Russell Labs, 1630 Linden Drive, Madison, WI 53706, USA.
E-mail address: cwood9@wisc.edu (C.M. Wood).

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developing effective ecosystem restoration practices that minimize short-term impacts to endangered species is a key to meeting both objectives. Developing rigorous analytical frameworks that quantify species–ecosystem tradeoffs in the currencies of population viability and restoration accomplishments under alternative management strategies would facilitate such efforts (Fraser et al., 2017).

Metapopulation theory and models have provided conceptual and analytical frameworks for conserving endangered species in fragmented landscapes for over two decades (Hanski, 1998; Levins, 1969; McCullough, 1996) and, we suggest, hold considerable promise for evaluating trade-offs between species and ecosystem conservation objectives. While prioritizing vacant patches for restoration is an intuitively appealing approach for minimizing effects on endangered species, metapopulation theory predicts that reductions in the quality of unoccupied habitat patches resulting from restoration practices reduces population viability (Hanski, 1998). That is, prioritizing patches for restoration based purely on occupancy status is challenging because patches in a metapopulation regularly switch between occupied and unoccupied states. Nevertheless, when targeting long-vacant patches for restoration carries relatively low risk, restoration may lead to metapopulation growth in the long-term (Lawson et al., 2014). A key question is: "how many years of vacancy are necessary before restoration can occur without reducing metapopulation viability?" The question "how do such thresholds influence the ability to meet restoration objectives?" is equally important given that requiring long vacancy periods before implementing restoration actions limits the fraction of a landscape that can be restored. For a vacancy threshold to be informative, a negative relationship must exist between the duration of patch vacancy and the probability that a vacant patch will be recolonized, otherwise the impacts of restoration to the overall metapopulation are expected to be independent of the time they are vacant.

The spotted owl (*Strix occidentalis*) is an ideal species for using metapopulation principles (particularly vacancy thresholds) to assess tradeoffs between conservation efforts oriented towards short- and medium-term objectives for focal species and those designed for longer-term ecosystem restoration objectives. Spotted owls' territorial behavior and strong site fidelity result in spatially structured populations whose dynamics are consistent with those of a metapopulation, where individual breeding pairs that occupy the same territories over a long time are analogous to a network of interacting local populations (Gutiérrez and Harrison, 1996). Moreover, populations of this species have been intensively monitored yielding multi-generational territory occupancy histories (Dugger et al., 2015; Franklin et al., 2000; Tempel et al., 2016, 2014). Most importantly, spotted owls reside at the epicenter of regional and national forest management debates that hinge on the tradeoffs between the retention of critical spotted owl habitat and forest restoration treatments. While spotted owl occupancy rates tend to be higher in territories containing greater amounts of the closed-canopy forest (Tempel et al., 2016, 2014), reducing tree densities with fuels reduction treatments in such stands are considered essential for reducing large, severe fires and drought-related tree mortality (Collins et al., 2010; Dow et al., 2016; Hagmann et al., 2017). Developing forest restoration practices that minimize the potential short-term costs of reducing habitat elements important to spotted owls while maximizing the flexibility to achieve forest resilience is imperative for achieving both ecosystem restoration and species conservation objectives (Peery et al., 2017). Moreover, developing criteria for selecting spotted owl territories (i.e., habitat patches) for ecosystem restoration without reducing viability of owl populations will facilitate this process.

We developed a Stochastic Patch Occupancy Model (SPOM) (Caswell and Etter, 1993; Gyllenberg and Silvestrov, 1994) to explore the potential impacts of treating unoccupied patches under alternative, hypothetical forest restoration strategies on the viability of a spotted owl "metapopulation." We evaluated forest restoration strategies that varied according to vacancy thresholds prior to restoration and the amount of owl habitat within territories treated. Our specific objectives were to: (1) leverage a 22-year territory occupancy dataset to assess the effects of habitat conditions and duration of territory vacancy on territory extinction and colonization rates, (2) use these statistical relationships to parameterize and implement SPOMs under different forest restoration strategies, and (3) explore trade-offs between projected changes in territory occupancy as a function of treatment frequency and number of territories treated under the different restoration strategies. We predicted that forest restoration involving shorter vacancy thresholds for treatments would result in greater declines in projected occupancy but that shorter vacancy thresholds would increase the frequency that treatments could be implemented within owl territories. This represented a simple yet novel metapopulation framework for explicitly quantifying trade-offs between the implementation of ecosystem restoration and predicted impacts to population viability that also would be applicable to development of species conservation guidelines in a range of ecosystems.

2. Methods

2.1. Territory occupancy surveys

We modeled occupancy histories of 64 spotted owl territories surveyed as part of a long-term demographic study area in the central Sierra Nevada, California (Fig. 1). We used annual territory occupancy histories from 1993 to 2014 based on surveys that followed standardized protocols (Forsman, 1983; Tempel et al., 2014). Briefly, we used vocal lures at established call stations and walking routes covering the entire area. We attempted to capture and band all located owls with unique color-coded combinations to identify owls at individual territories. We considered territories occupied when at least one owl was detected during daylight or twilight hours within or near (< 400 m) the known core area, and reduced false positives as recommended by Berigan et al. (2018). We excluded nocturnal detections from unidentified individuals because they may not be territory holders.

2.2. Modeling patterns in territory extinction and colonization

We included territory occupancy histories in the analysis beginning in the year a territory was first determined to be occupied and that also had uninterrupted survey effort through 2014. These two criteria ensured that any recolonization events would occur with a known number of years preceding vacancy. We used the same definitions for extinction and (re)colonization as MacKenzie et al. (2003). We did not use a formal multi-season occupancy modeling approach because detection probabilities for bimonthly survey periods have been estimated to be 0.68 (Tempel et al., 2016), which, over the four-month season, yields an overall detection probability of 0.99. Therefore, we assumed perfect detection and treated the annual survey results as true presence/absence data. We used binomial logistic regression to model associations between extinction and, separately, colonization and predictor variables (described below), which is mathematically equivalent to the process MacKenzie et al. (2003) used to test the influence of covariates on those same probabilities. Our process of estimating extinction and recolonization rates was therefore effectively equivalent to that used to obtain detection-corrected estimates of those rates.

We treated the number of years of consecutive preceding vacancy and the amount of owl habitat within 400-ha circular areas (i.e., ~territory size; Tempel et al., 2016) as predictor variables in the recolonization logistic regression. Our habitat variable was the proportion of a territory comprised of forests having both ≥70% canopy cover and trees with a quadratic mean diameter-at-breast height (QMD) ≥ 61 cm (hereafter referred to as "owl habitat"). We extracted habitat data from gradient nearest-neighbor (GNN) structure maps, which use Landsat imagery informed by forest measurements taken at Federal Inventory and Analysis (FIA) plots to give 30 m coverage of the