Feature Articles

MEXICAN SPOTTED OWLS USE FOREST MOSAICS AFFECTED BY TIMBER HARVEST, INSECTS, AND WILDFIRE

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ABSTRACT–Understanding how species of conservation concern interact with natural disturbances provides insights into their evolutionary environment and can inform land management and conservation planning. We examined the breeding season nocturnal space use (i.e., foraging ecology) of three Mexican spotted owls (*Strix occidentalis lucida*) in southern New Mexico, USA that occurred in areas previously affected by timber harvest, wildfire, and insect-related tree mortality, respectively. We found that individual owls (1) preferentially used the ecotone between forests that were harvested and those that were not; (2) avoided severely-burned forest but used areas with mixtures of different burn severities (i.e., 'pyrodiversity'); and (3) heavily used a small patch of insect-killed forest that resulted in extensive downed woody debris. In sum, forests characterized by a mixture of stand ages and stages, produced by various mechanisms, were consistently and preferentially used by Mexican spotted owls. Mexican spotted owl use of heterogeneous forest environments makes sense in light of historical disturbance regimes of this region, which were characterized by frequent lower severity fire events that generated spatial and temporal landscape heterogeneity.

RESUMEN— Comprender cómo las especies de preocupación para la conservación interactúan con las perturbaciones naturales proporciona información sobre su entorno evolutivo y puede informar el manejo de la tierra y la planificación de la conservación. Examinamos el uso del espacio nocturno durante la temporada de reproducción (es decir, la ecología alimentaria) de tres búhos manchados mexicanos (*Strix occidentalis lucida*) en el sur de Nuevo México, EE. UU., que ocurrieron en áreas previamente afectadas por la tala, los incendios forestales y la mortalidad de árboles relacionada con insectos, respectivamente. Encontramos que los búhos individuales (1) preferían usar el ecotono entre los bosques que fueron talados y los que no; (2) evitaron los bosques severamente quemados pero utilizaron áreas con mezclas de diferentes severidades de quema (es decir, "pirodiversidad"); y (3) utilizaron intensamente un pequeño parche de bosque afectado por insectos que resultó en una gran cantidad de residuos leñosos caídos. En resumen, los bosques caracterizados por una mezcla de edades y etapas de rodal, producidos por diversos mecanismos, fueron utilizados de manera consistente y preferencial por los búhos manchados mexicanos. El uso de entornos forestales heterogéneos por parte del búho manchado mexicano tiene sentido a la luz de los regímenes de perturbación históricos de esta región, que se caracterizaron por frecuentes eventos de incendios de baja severidad que generaron heterogeneidad espacial y temporal del paisaje.

In western North America, forest landscapes are experiencing changes in disturbance regimes that represent departures from the historical range of variability (Hagmann et al., 2021). These include larger, more severe, and more frequent wildfire events (Parks & Abatzoglou, 2020), insect and disease outbreaks resulting in widespread tree mortality (Anderegg et al., 2015), and droughts that are more intense, more extensive, and longer-lasting (Asner et al., 2015). In some forest ecosystems, fuels-reduction and forest-restoration activities can increase the resilience of forests to these drivers (Koontz et al., 2020; Stephens et al., 2021; Young et al., 2017). But fuels reduction and forest restoration have the potential to alter the habitat of sensitive and/or threatened mature-forest-dependent and old-forest-dependent species, most notably spotted owls (*Strix occidentalis*) (Ganey et al., 2017). Understanding how spotted owls and other mature-forest-dependent and old-forest-dependent species interact with disturbance-created

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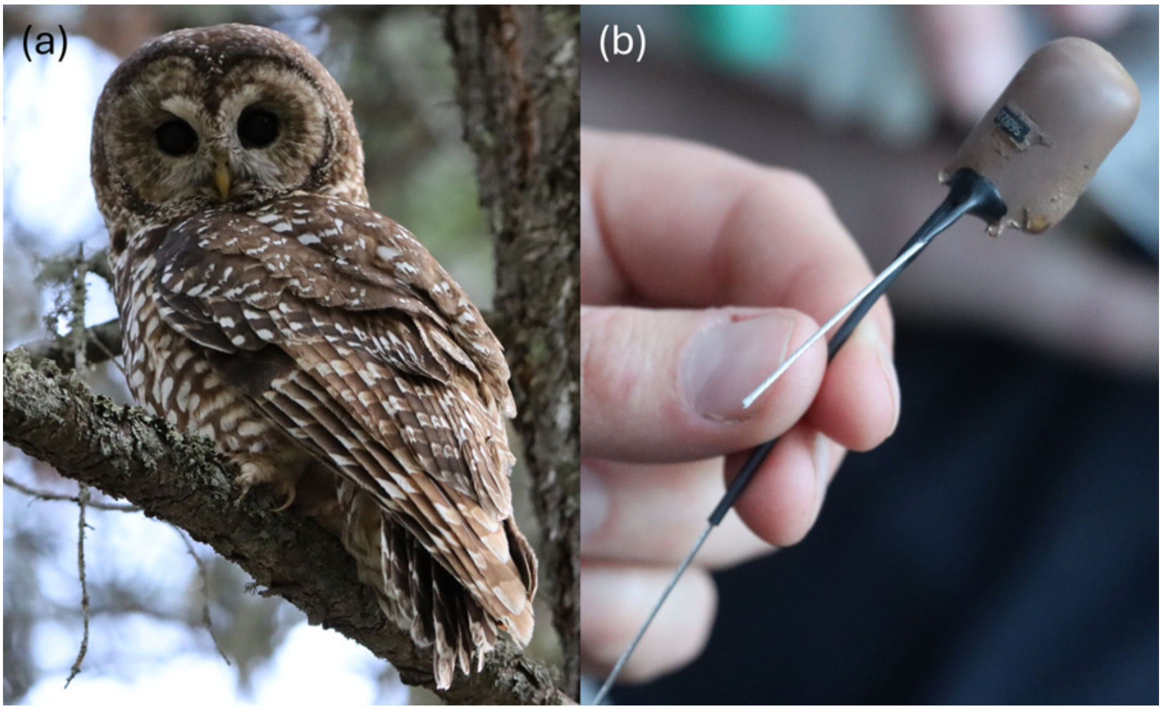

FIG. 1. (a) Adult Mexican spotted owl (*Strix occidentalis lucida*) captured as part of our ongoing GPS tagging study in Arizona and New Mexico. (b) One of the Lotek Pinpoint 120 GPS tags used as part of this study. Photos by Doug Fitzpatrick/University of New Mexico/USDA Forest Service.

conditions, such as severely burned forest, insect-killed forest, and forests that have experienced fuels-reduction activities (e.g., tree thinning, prescribed fire), is important for improving species-conservation practices in the face of global change.

In the summers of 2023 and 2024, we captured three Mexican spotted owls (*Strix occidentalis lucida*) (Fig. 1) in the Sacramento Ranger District of the Lincoln National Forest, in southern New Mexico, and tracked their movements using tail-mounted GPS units (Pinpoint 120, Lotek, Inc., Seattle, WA) (Kramer, Jones, Kane, et al., 2021). These individuals represented a subsample from a much larger GPS-tracking study that is ongoing across portions of Arizona and New Mexico; we selected these three individuals to highlight their interesting interactions with a variety of disturbance events that affected forest structure and vegetation succession in their home ranges. The disturbances occurred 10-24 years prior to GPS tagging, and our results thus reflected implicit interactions between disturbance and time (i.e., vegetation succession). We programmed the GPS tags to collect a location once per hour daily during nocturnal hours (from 2100 to 0500 h) between April and July of each year. GPS locations could reflect a range of owl behaviors, including territorial movements, forays, hunting, and other behaviors. However, because all three of the male owls observed in this study were part of a nesting pair, it is likely that a large portion of their nocturnal movements represented hunting activities pursued to provision offspring.

Across the three owls used in this study, the GPS tags collected between 128 and 435 locations over a period of 23 to 69 days, respectively. In addition to attaching GPS tags, we fitted each owl with a US Geological Survey (USGS) aluminum leg band on one leg and a unique-color band on the other leg. We conducted all the surveys, captures, and handling of Mexican spotted owls with valid state and federal permits (USGS Federal Bird Banding Permit #24395; US Fish and Wildlife Service Permit #ESPER0036384; New Mexico Department of Game and Fish Permit #3831).

We used integrated step-selection analysis (iSSA; Avgar et al., 2016), now a widely used approach in animal habitat-selection studies, to model habitat selection while accounting for correlated movements. For each step (i.e., each GPS point in a sequence of nightly movements), we randomly generated 10 available locations based on a distribution of step lengths and turn angles using the R package amt, version 0.2.2.0 (Signer et al., 2019). The combination of 1 "used" location with 10 "available" locations formed a stratum for conditional logistic-regression analysis. We then fitted models using the R package glmmTMB, version 1.1.9 (Brooks et al., 2024), and applied the model-fitting recommendations of Muff et al. (2020).

We fitted an individual iSSA model for each individual bird, including fixed-effects terms for step length, turn angle, cosine of the turn angle, and the focal variable or variables for each individual (treatment, fire, or insect-caused mortality). Stratum was treated as a random effect. The response variable was binary: 0 represented available locations, and 1 represented used locations; the resulting fitted model predicted the relative probability of use. We explored linear or quadratic effects for each focal variable and reported the functional form that resulted in a fitted model with lower Akaike Information Criterion (AIC). If linear and quadratic models were very similar in terms of AIC (within ~1 unit), we reported the linear effect only. In addition, we used a stratum-specific intercept term as a random effect and fixed the variance on this random effect to 1,000 (Muff et al., 2020).

We summarized covariates (area treated, burn severity, and insect-caused tree mortality) in a circular buffered area surrounding each GPS point with a radius of 100 m (approximately 7.8 acres). We thus interpreted treatment and insect-caused-mortality covariates as the proportion of buffered area containing that feature. Fire covariates represented the mean value in the buffered area. We initially determined the spatial features, type of prescription, and completion date using the USDA Forest Service's Forest Activity and Tracking System and validated them with local forest staff. We determined burn severity using the USGS Monitoring Trends in Burn Severity dataset, and we computed pyrodiversity as the standard deviation in burn severity (Jones & Tingley, 2022). We calculated insect-caused mortality by mosaicking multiple independent datasets that estimated defoliation events and validated it with a field trip to the area of interest. The final shapefile representing insect-caused mortality was hand-digitized using a combination of aerial imagery, cross-referencing with other geospatial datasets, and expert opinion provided by local forest biologists.

The first owl we captured had a home range that overlapped with a 2013 fuels-reduction treatment (Fig. 2a). The treatment involved a timber harvest that resulted in an open-canopy cut (hereafter treated area) in accordance with the revised 2012 Mexican Spotted Owl Recovery Plan (U.S. Fish & Wildlife Service, 2012). Briefly, mechanical thinning was used to create canopy openings from 0.5 to 1 acre across portions of the treated area, and to produce uneven aged forest structure and irregular patch spacing to mimic natural disturbance patterns. To date, little is known about how spotted owls of any subspecies interact with areas that have previously been treated for fuels reduction (but see Gallagher et al., 2018). Our results showed that this male owl preferentially used treated areas within its home range (β_x = 6.67, 95% confidence interval (CI) = [4.14, 9.21]), up until approximately 50% of the buffered area contained treatment, at which point relative probability of use declined (β_{x^2} = −7.03, 95% CI = [−10.12, −3.93]) for presumed foraging/hunting activities (Fig. 2b). The treated area was characterized by coarse woody debris, tree stumps, and intermixed patches of closed-canopy and open-canopy forest (Fig. 2c). It is important to note that the larger treated-area patch that was heavily used in the southwestern portion of this owl's home range was relatively small (only 96 acres). Thus, we cannot extrapolate our results to how spotted owls might use treated areas of smaller or larger spatial extents or of different configurations.

The second Mexican spotted owl had a home range that overlapped with the ~20,700-acre Scott Able Fire of the year 2000 (Fig. 3). Research on the California subspecies of spotted owl (*Strix occidentalis occidentalis*) has shown that owls avoid extensive areas of severely burned forest for foraging but use smaller patches preferentially (Jones et al., 2020; Kramer, Jones, Whitmore, et al., 2021). Our results suggested that this owl had similar patterns of space use, avoiding extensive areas of severely burned forest (β_x = −2.23, 95% CI = [−3.03, −1.43]) (Fig. 3a) and, when it did enter the large, severely burned patch of forest, traveling a maximum of only 100 m into it (Fig. 3c). Moreover, this owl preferentially used areas of high pyrodiversity (β_x = 8.03, 95% CI = [3.83, 12.22]) or places where multiple burn severities were spatially juxtaposed (Fig. 3a). This effect was nonlinear, however, plateauing and slightly declining at very high levels of pyrodiversity (β_{x^2} = −5.52, 95% CI = [−9.53, −1.51]). Pyrodiverse areas within this owl's home range tended to be characterized by patches of live forest positioned next to patches of fire-killed forest (Fig. 3b, 3c).

Finally, the third owl observed in this study occurred in an area that experienced an insect-driven defoliation event between 2004 and 2005 that resulted in the mortality of trees across an area of approximately 6 acres (Fig. 4). To our knowledge, no studies have reported interactions between spotted owls and insect-killed forest stands. Our results suggested that this owl preferentially used the 6-acre patch of forest that was killed by defoliators (β_x = 5.43, 95% CI = [3.85, 7.01]) (Fig. 4a). As with our results for the first owl, we cannot infer effects of larger patches of insect-killed trees. However, we can state with confidence that this individual spotted owl used this small patch of insect-killed forest preferentially (Fig. 4b). The vegetation conditions in this patch were characterized by a high density of standing dead trees (i.e., snags) and extensive downed woody debris, surrounded by mature mixed-conifer forest with open understory around the edge of the patch (Fig. 4c).

Forests in the southwestern USA have experienced natural disturbances such as wildfire and insect-caused mortality for millennia (Hessburg et al., 2019). Our results suggested that the nocturnal space use of Mexican spotted owls (e.g., indicative of foraging habitat) appears to align with characteristics that are consistent with the region's historical disturbance regimes. Regarding wildfire, the individual owl whose home range overlapped with the Scott Able Fire of 2000 tended to use areas that were burned less severely and that had a more diverse mosaic of burn severities (Fig. 3). These conditions would have been historically common in low-to-mid-elevation conifer forests in the southwestern USA (Kaye & Swetnam, 1999). Insect-caused tree mortality is also a natural driver of landscape dynamics in these forests, and the individual owl that was exposed to a small area of insect-caused tree mortality used it heavily (Fig. 4). Mexican spotted owls are likely favoring the use of mosaics created by wildfire and insects because they generate vegetation heterogeneity and successional diversity, which support the presence of diverse prey communities that can influence the fitness of spotted owls (Kuntze et al., 2023).

Though historically unnatural, timber harvest can produce similar patterns of forest heterogeneity that support the prey habitat of spotted owls (Fig. 2). Thus, Mexican spotted owls may use forests affected by timber harvests that have a limited spatial extent (i.e., small-scale harvests) for the same reason they use forests affected by wildfire and insects: abundant access to food resources. Therefore, the important factor may be not the agent of disturbance but rather the vegetation patterns resulting from disturbance of any kind. The quadratic effect shown in Fig. 2b indicates that the owl was more likely to use the ecotone between treated and untreated areas (where ~50% of the buffered area contained treatment), which is consistent with research suggesting that smaller-scale timber harvests may

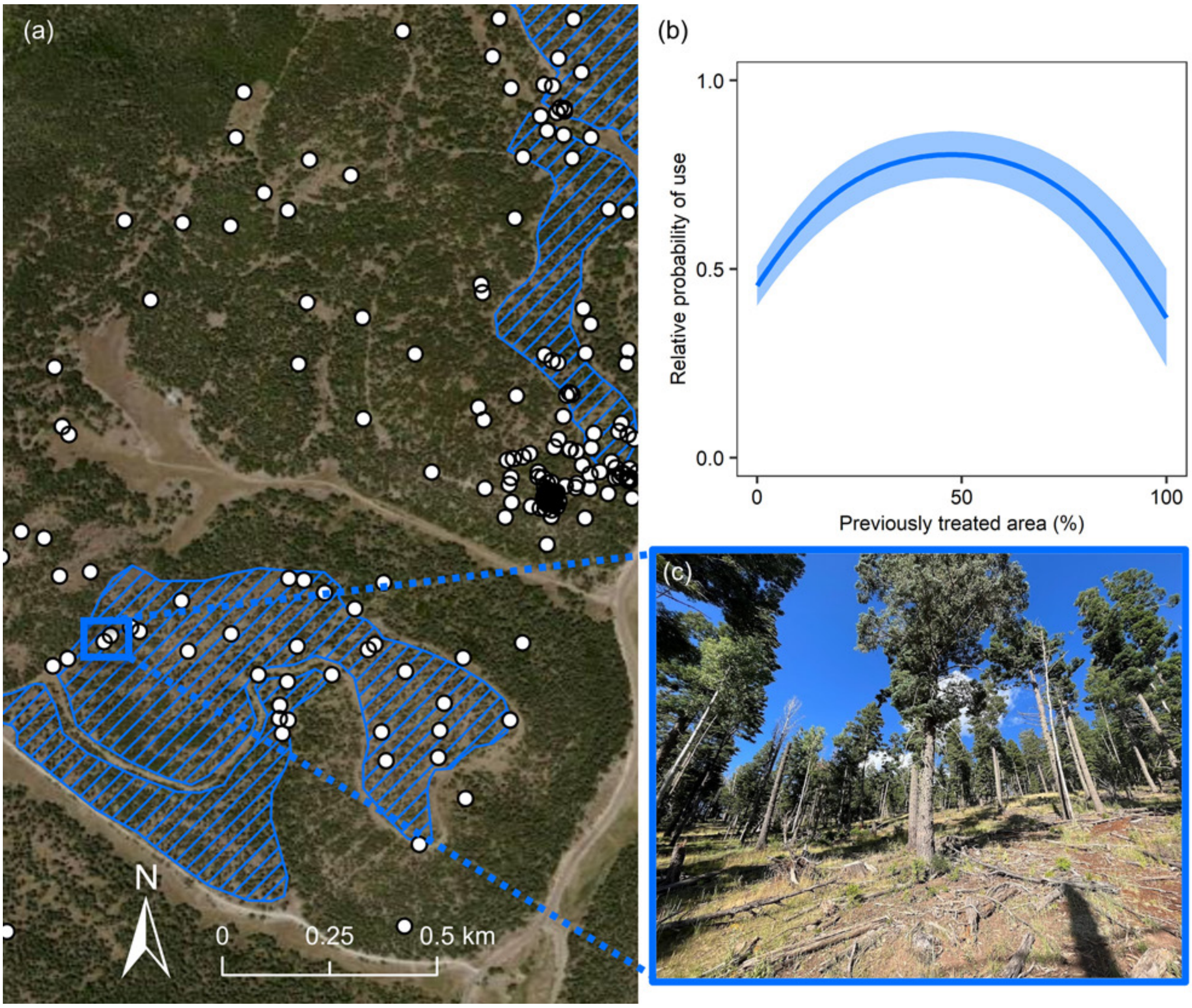

FIG. 2. Interactions between a Mexican spotted owl (*Strix occidentalis lucida*) and a previously treated area. (a) GPS points are indicated by white dots and treated areas by blue hatch marks. The treated area in the lower left had undergone an improvement-cut treatment, and the area in the upper right had undergone a precommercial-thinning treatment. For our analysis, we pooled these types of treatment into a single treatment category. (b) The predicted relationship between area treated and relative probability of use for this individual owl. (c) Photo taken within the treated area near a location where this owl putatively hunted for prey. Photo by Gavin Jones/USDA Forest Service.

benefit the foraging ecology of spotted owls (Zulla et al., 2023).

Historically, frequent fire regimes in this system resulted in a great deal of spatial and temporal heterogeneity in forest age and structure (Swetnam et al., 1999), which shaped evolutionary adaptations in animals to maximize their fitness (Pausas & Parr, 2018). Fire exclusion and logging have produced widespread homogenization of forest conditions that may be historically novel, and restoration of heterogeneity might be achieved through a variety of management activities, including prescribed fire and forest thinning (Reynolds et al., 2013). More research must be done to understand the variety of ways in which forest-management activities, including precommercial and commercial thinning, mastication, and prescribed fire, influence prey communities of the Mexican spotted owl and, by extension, its space use and fitness. Our study of three owls selected from a larger subsample of tagged birds provides some initial evidence that Mexican spotted owls appear to benefit from forest heterogeneity introduced by a variety of causes, including timber harvest.

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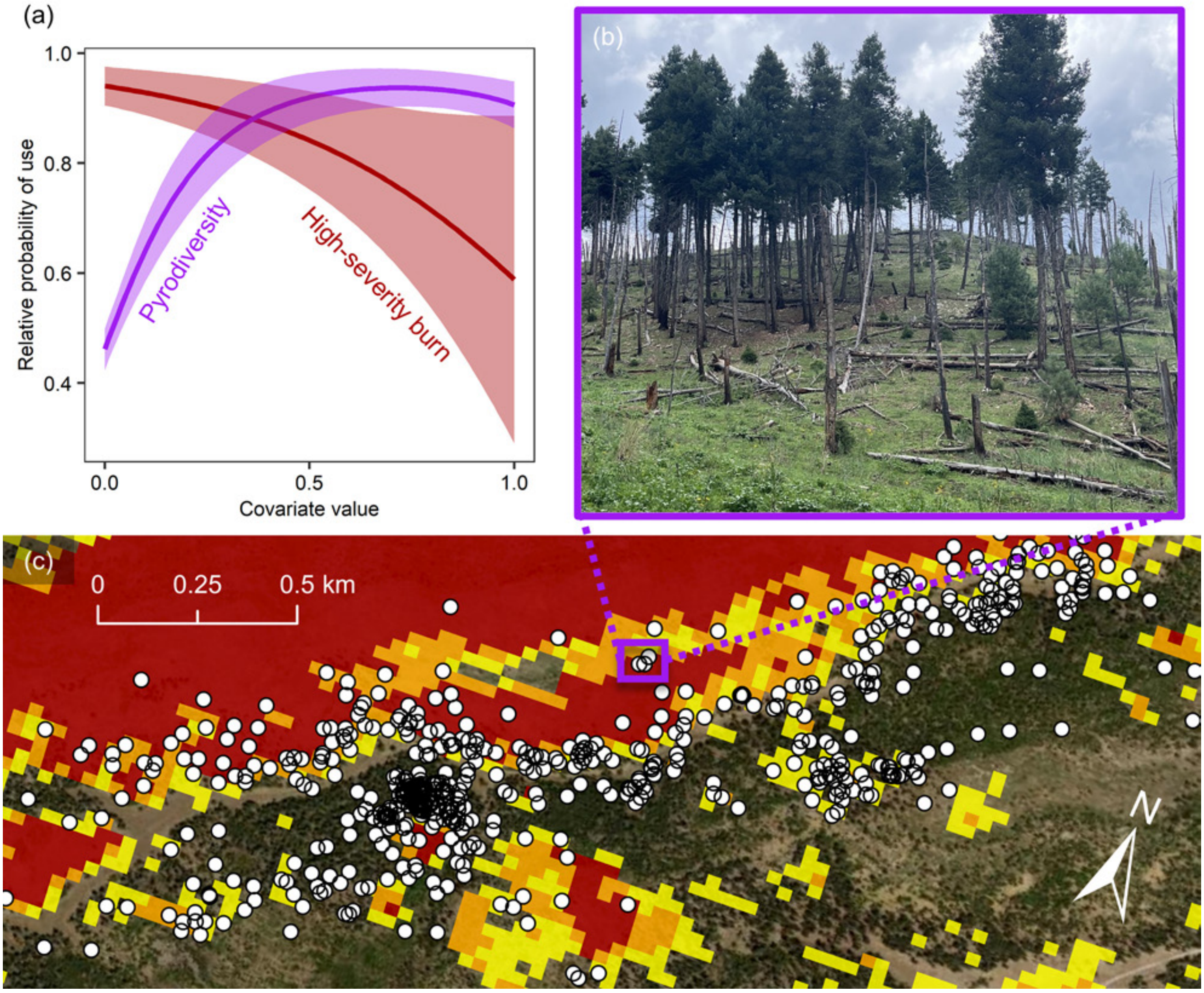

FIG. 3. Interactions between a Mexican spotted owl (*Strix occidentalis lucida*) and a previously burned area. (a) Inverse relationships between high-severity burn and pyrodiversity, showing avoidance of areas with more extensive high-severity burn and selection of more pyrodiverse areas. For high-severity burn, the x-axis represents the proportion of the buffer containing high-severity burn; for pyrodiversity, the x-axis represents a rescaled pyrodiversity index ranging from 0 (lack of diversity of burn severities) to 1 (high interspersion of burn severities). (b) Example of the forest structure observed in a highly pyrodiverse area where this owl spent time foraging (Photo by Gavin Jones/USDA Forest Service). (c) GPS points showing seasonal movements of this owl at the perimeter of the 2000 Scott Able Fire. Red areas represent high-severity burn (>75% canopy mortality), orange areas represent moderate-severity burn (25-75% mortality), and yellow areas show low-severity burn (<25% mortality).

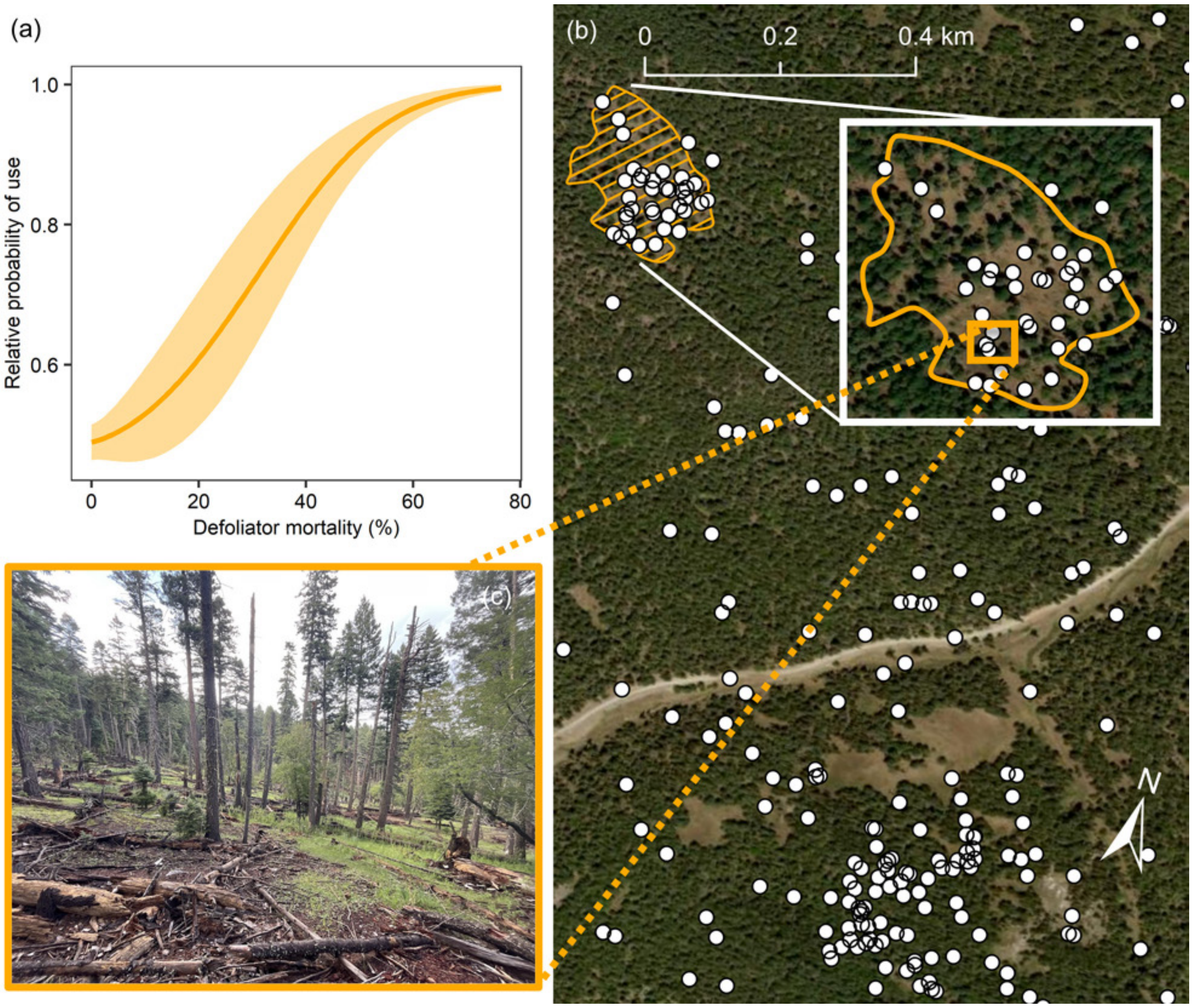

FIG. 4. Interactions between a Mexican spotted owl (*Strix occidentalis lucida*) and a forest stand killed by insects in the early 2000s. (a) Relationship between defoliator-killed trees and relative probability of use for this small, 6-acre patch. The x-axis represents the proportion of the buffered area containing defoliator mortality. (b) GPS points are indicated by white dots and the insect-affected area by orange hatch marks. The inset photo in (b) provides an expanded image of the high density of owl locations and the open nature of the area. (c) Photo taken from within the stand of trees killed by insects. Photo by Gavin Jones/USDA Forest Service.

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