Multi-year nest box occupancy and short-term resilience to wildfire disturbance by barn owls in a vineyard agroecosystem

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Abstract. Landscape composition can strongly affect the delivery of ecosystem services in agroecosystems. Conserving uncultivated habitats can support ecosystem services, but in Mediterranean biomes, these lands can also increase the area susceptible to wildfires. In the world-renowned wine-producing region of Napa Valley, California, wine grape growers install nest boxes to attract American barn owls (Tyto furcata), which may reduce rodent crop damage. Annual monitoring of 273 nest boxes began in 2015, and devastating wildfires burned approximately 60,000 ha in the region in 2017, including homes and businesses, as well as some vineyards and uncultivated land. The goal of this study was to determine whether changes in nest box occupancy were attributed to wildfires, nest box design, land cover type, or some combination of these variables. Occupancy surveys before and after these wildfires revealed changes in habitat selection at the nest scale. Occupancy increased during the study, reaching its highest point after the fire. Owls were found breeding in recently burned areas that were previously unoccupied and modeling results showed that nest box occupancy had a positive relationship with burned areas, particularly with edges of the fire perimeter. Barn owls also consistently showed a strong preference for taller nest boxes that were surrounded by more grassland than other land cover types and a moderate selection for wooden over plastic boxes. These results illustrate an incentive for the conservation of uncultivated habitat, particularly grassland, in vineyard ecosystems, and they provide an example of a mobile pest predator’s response to wildfire disturbance. In this case, results suggest an agroecosystem service made resilient to wildfire by the owls’ selection of burned and uncultivated habitats.

Key words: Barn owl; colonization; habitat selection; landscape; nest box; occupancy; Tyto alba; Tyto furcata; vineyard; wildfire.

INTRODUCTION

Landscape composition has become a major focus for understanding the provisioning of ecosystem services in agroecosystems (Tscharntke et al. 2005). With threats of climate change and habitat loss, there is increasing interest in optimizing landscapes for both conservation and crop production (Kremen and Merenlender 2018, Garibaldi et al. 2020). Uncultivated habitat that
harbors greater biodiversity has been connected to enhanced delivery of ecosystem services such as pest control in agricultural landscapes (Boesing et al. 2017). Conserving uncultivated habitats can support ecosystem services, but in fire-prone ecosystems, these lands can also increase the area susceptible to wildfires (Westerling et al. 2006). Understanding the interactions between landscape composition, ecosystem services, and disturbance is necessary to ensure ecosystem services can be optimized.

Landscape composition affects nest site selection by barn owls (Tyto alba and Tyto furcata), a biological control agent, which has implications for their potential to deliver rodent pest control in crop systems worldwide (Hafidzi and Mohd 2003, Meyrom et al. 2009, Kross et al. 2016, Wendt and Johnson 2017). In the world-renowned vineyard ecosystems of Napa Valley, California, rodent pests can cause millions of dollars in crop damage annually (Baldwin et al. 2014). Vineyard managers often use lethal trapping and chemical rodenticides, but these solutions are labor-intensive and cause concern over secondary poisoning to humans and wildlife (Marsh 1992, Baldwin et al. 2015, 2017). The need to control rodent pests has led to an interest in integrated pest management using biological control agents, primarily barn owls (Labuschagne et al. 2016). By installing nest boxes in vineyards, farmers can attract barn owls, which may be able to act as natural predators and reduce populations of rodent pests (Meyrom et al. 2009, Paz et al. 2012, Kan et al. 2013, Browning et al. 2017). However, barn owls are mobile predators and they show a preference for open natural habitats (Taylor 1994), so the effectiveness of nest box installation on pest control delivery may depend on the composition of landscapes surrounding wine grape vineyards (Chartier et al. 2012). In Napa Valley, American barn owls (Tyto furcata) are most likely to occupy nest boxes with uncultivated habitats within 1 km, along with preferences for nest boxes constructed of wood, facing away from the sun, and installed at least 3 m above ground (Wendt and Johnson 2017). Barn owls nesting on vineyards also preferentially hunt in uncultivated habitats, selecting them over more closely available vineyards (Castañeda 2018).

After wildfires burned nearly 60,000 ha in Napa Valley in 2017, many uncultivated lands that barn owls prefer were dramatically altered. The fires primarily burned through grasslands, wooded areas, and communities surrounding vineyards (Lapsley and Sumner 2017). Mediterranean biomes, like that of Napa, evolved with fire, though changing climate and fire suppression are increasing the likelihood and severity of fires (Batllori et al. 2013). Additionally, much of California, including Napa, is experiencing conversion of native perennial grasses to nonnative annual grasses, which increase the availability of fine fuels and thus increase fire frequency (Jurjavec et al. 2002, Keeley and Brennan 2012). In the whole western United States, wildfires have increased in both frequency and intensity since the mid-1980s, which is primarily attributed to warming, earlier springs (Westerling et al. 2006), and fuel accumulation (Westerling et al. 2003, Agee and Skinner 2005), making this a critical time to understand the impact of wildfires on landscapes and ecosystem services.

With changes to the landscape caused by wildfires, we hypothesized that barn owls would respond by nesting near recently burned uncultivated habitats. Barn owls prefer open habitat and fires have the potential to reduce the structure of denser habitats, so we posited that the wildfires in Napa Valley could provide more land that is ideal for barn owl hunting. Additionally, while small mammal responses are variable, rodents can increase in recently burned areas (Schwilk and Keeley 1998, Fitzgerald et al. 2001). In other recently burned Mediterranean climates, fires produced edge habitat and open areas that may be preferred by rodents (Haim and Izhaki 1994, Torre and Díaz 2004).

To our knowledge, this is the first study to address how wildfire may affect the distribution of a mobile agent of an agroecosystem service. Barn owl nest site selection in relation to landscape composition is important for both short-term understanding of resiliency to wildfire disturbance and long-term expectations for the potential of barn owls to act as a natural enemy in agriculture. Nest box occupancy is dynamic in nature and fluctuates from year to year (Chartier et al. 2018). Understanding barn owl breeding behavior in relation to habitat in
average years and after disturbance is important for management and knowledge of barn owl behavior.

**Methods**

**Study area**

This project took place on vineyards in Napa Valley, California (surrounding city of Napa, 38.3° N, 122.3° W). The valley is ~48 km long and 5–20 km wide and is characterized by a Mediterranean climate ideal for growing grapes (Napa Valley Vintners 2017). Mixed oak woodlands and oak savannahs are spread throughout the region, with grasslands common in the south and mixed oak scrub and conifer forests more common in the north (Napa County 2010, Wendt and Johnson 2017). The unique conditions in Napa Valley have created a wine industry which generates $3.7 billion in annual revenue and in combination with tourism, employment, and distribution, is estimated to have an annual impact of $50 billion on the American economy (Stonebridge 2012).

The Atlas, Nuns, and Tubbs fires burned nearly 60,000 ha surrounding Napa Valley in October 2017 (California Department of Forestry and Fire Protection 2017a, b, c; Fig. 1). Evidence indicates they were ignited during a spike in fire risk (i.e., low humidity, high temperatures, and unseasonably high warm winds; Martinez et al. 2017) and were extinguished after extensive and costly fire control (Associated Press 2018). Like other wildfires in the western United States, they burned in patches of various degrees of fire severity within an irregular fire perimeter, introducing fire-caused vegetation heterogeneity in the following spring and summer. In October, vineyards have lower fuel loads than most surrounding natural habitats, many are also irrigated, and fire suppression activities prioritized human structures. Thus, few vineyards were actually burned by these fires, with most fire occurring in oak savannah, grassland, and other uncultivated land cover types (Lapsley and Summer 2017). The heterogeneity in vegetation after fire did not include conversion of any land cover type to another, but included a mixture of burn severity throughout the burned area, resulting in variability in the state of soils and vegetation (California Department of Forestry and Fire Protection 2017c).

**Study species**

The barn owl is a widespread raptor species that will readily nest in human-made structures and is adapted to hunt in open grasslands and agricultural fields (Taylor 1994). In Napa Valley, natural nesting cavities are not readily available, as the diameter of most trees is too small (Grossinger 2012) and where larger trees exist, American barn owls are subject to predation from great-horned owls (*Bubo virginianus*; Millsap and Millsap 1987). Thus, barn owls in Napa readily make use of nest boxes in vineyards (Wendt and Johnson 2017). They are tolerant of their own species and can nest in high concentrations (Taylor 1994, Meyrom et al. 2009, Browning et al. 2017). Because of these qualities and their tolerance of humans, barn owls have been used as a means of rodent control for various crops including alfalfa, rice, oil palms, cocoa, and grapes in countries including Israel, Malaysia, Spain, South Africa, and the United States (Labuschagne et al. 2016). Though their ability to meaningfully control rodent populations remains a debated topic (Johnson et al. 2018), over 90% of their diet is composed of rodent pests and the number of rodents they remove is estimated to be substantial (Browning et al. 2017, St. George 2019). The primary prey of barn owls in Napa Valley includes the pest species voles (*Mictrous spp.*), pocket gophers (*Thomomys bottae*), and mice (*Mus musculus* and *Peromyscus spp.*), and the average occupied nest box consumes approximately 1,000 rodents throughout the breeding season (St. George 2019).

**Establishing nest box occupancy**

After a nest box occupancy study of 297 nest boxes began in 2015 (Wendt and Johnson 2017), a random sample of 150 boxes were monitored in 2016 and 2017. In 2018, we monitored all of the original 297 boxes for a comparative analysis of occupancy after the fires. The methods for the occupancy survey followed those of Wendt and Johnson (2017) and are briefly summarized here.

We visually inspected nest boxes with a GoPro camera and LED light attached to an extendable pole that we inserted into the opening of the nest box, viewing the contents via a live feed to a handheld smartphone. A nest box was considered occupied if, at any point in a season, it contained barn owl eggs or nestlings. Barn owls are
known to start courting in January, and in southern California, clutches generally begin in February (Marti et al. 2005). Eggs are laid in intervals of 2–3 d for a mean clutch size of about 5, taking about 10–15 d to complete a clutch, and incubation lasts for 29–34 d (Marti et al. 2005). Nests were checked every 10 d between 28 February and 31 March for breeding occupancy by barn owls. After the initial three checks throughout the month of March, any boxes with evidence of possible occupation were monitored monthly at least three more times to determine or confirm occupancy. Because of this timing and protocol, it is very unlikely that an occupied box went undetected during our timeframe for occupancy checks; using multi-season occupancy modeling, we estimated overall detection probability at over 97% (A. Huysman, unpublished data), so we did not further model detection probability. Though barn owls can double brood in some locales (Bank et al. 2019), our work focused on first breeding attempts. Like other species of birds, barn owls can be sensitive to disturbance and potentially abandon their nest, but if care is taken there should be no effect on the bird’s nesting productivity (Taylor 1991), and our camera-enabled remote monitoring procedure caused minimal disturbance (M. Johnson, unpublished data).

Analysis methods
Of the original 297 boxes monitored in 2015, 24 were broken ($n = 11$), removed ($n = 8$), or burned ($n = 5$) by 2018 and were excluded.
from analysis for all years. We used a multi-season occupancy model on the final sample of 273 nest boxes to evaluate the likelihood that alternative combinations of predictor variables affected occupancy, colonization, and extinction of nest boxes. In the context of this study, $\Psi$ (initial occupancy) represented the probability of a box being occupied during the first year of the study (2015), $\gamma$ (colonization) represented the probability of an unoccupied nest box becoming occupied each year until 2018, and $\varepsilon$ (extinction) represented the probability of an occupied nest box becoming unoccupied each year until 2018. We used the colect function from the unmarked package (Kény and Chandler 2016) in program R version 3.5.1, which fits multi-season occupancy models as described by MacKenzie et al. (2003). Because the nature of this study system allowed us to determine with near-perfect detection if a nest box is occupied, we fit these models with detection probability fixed equal to one.

We built our candidate model set using combinations of five predictors of land cover, three predictors of nest box design, and four predictors of wildfire (Table 1). The predictors were chosen based on the results of Wendt and Johnson (2017), which revealed that only home range scale and several nest box design predictors were significantly correlated with occupancy. Land cover and wildfire predictors were calculated based on a 2.81 km radius, which is the mean maximum distance moved by GPS tracked barn owls in this population (Huysman 2019). The land cover variables were created using a combination of remote sensing using NAIP (USDA 2009) and LiDAR (NSF 2013) and existing GIS layers (County of Napa 2010, USDA and NASS 2019) to classify land cover into seven categories at 4 m resolution: water/wetland, urban, vineyard, grassland, oak savannah, forest, riparian, and uncultivated.

Table 1. Description and justification for inclusion of covariates in multi-season occupancy model.

| Covariate      | Description                                                                 | Justification                                                                 |
|----------------|-----------------------------------------------------------------------------|-------------------------------------------------------------------------------|
| Home range scale | Vineyard                                                                 | Percent of vineyard within 2.81 km of nest box                               | Wine producers are interested in maximizing time spent in vineyard            |
|                | Grassland                                                                  | Percent of grassland within 2.81 km of nest box                              | Found to be significant predictor of both occupancy† and hunting habitat selection‡ |
|                | oakSavannah                                                                | Percent of oak savannah within 2.81 km of nest box                           | Found to be significant predictor of both occupancy† and hunting habitat selection‡ |
|                | Forest                                                                     | Percent of mixed forest within 2.81 km of nest box                           | Found to be significant predictor of occupancy†                              |
|                | Riparian                                                                   | Percent of riparian within 2.81 km of nest box                              | Found to be significant predictor of occupancy†                              |
|                | Uncultivated                                                              | Percent of vineyard, grassland, oak savannah, and mixed forest within 2.81 km of nest box | Combination of uncultivated habitat has potential to provide a more parsimonious explanation of occupancy |
| Box scale      | box_material                                                               | Nest box material (plastic or wood)                                         | Found to be significant predictor of occupancy†                              |
|                | entr_dir                                                                   | Binary variable: toward or away from sun                                     | Found to be significant predictor of occupancy†                              |
|                | ht                                                                         | Distance in m from bottom of the nest box to the ground                     | Found to be significant predictor of occupancy†                              |
|                | Fire                                                                       |                                                                                  |                                                                                  |
|                | amtBurned                                                                  | Percent of area burned within 2.81 km of nest box                           | Represents total area available to the owl for hunting that was impacted by fire |
|                | outerFireEdge                                                              | Length of fire perimeter (km) within 2.81 km radius of nest box             | Owls hypothesized to use edge of fire perimeter because rodents will be recolonizing and tree cover will be less dense in burn |
|                | fireSeverityEdge                                                           | Length of edge (km) between areas of low severity and higher severity fire within 2.81 km radius of nest box | Edge between different levels of fire severity will likely function similarly to edge between burned and unburned areas |
|                | distToFire                                                                 | Distance from nest box to fire edge                                          | Owls will likely use the fire edge if it is more accessible from the nest box |

† Wendt and Johnson (2017).
‡ Castañeda (2018).
grassland, oak savannah, mixed forest, and riparian. Only five of these land cover categories were used in modeling (Table 1). Soil burn severity and fire edge data were obtained from Cal Fire (California Department of Forestry and Fire Protection 2017a, b, c). To avoid multicollinearity, no variables with a correlation coefficient of 0.8 or greater were included in the same sub-model structure.

We built our candidate model set using a secondary candidate set strategy where we created a candidate model set for each sub-model (initial occupancy, colonization, and extinction) before using the top models from each sub-model set for a final candidate model set (Morin et al. 2020). Each candidate sub-model represented a different hypothesis about which combination of land cover, nest box design, and wildfire predictors would best explain each parameter in the multi-season occupancy model. The sub-models included 18 candidate models for occupancy, 97 models for colonization, and 97 models for extinction (Appendix S1). We reasoned that any variables that could be hypothesized to affect colonization could also affect extinction and therefore the colonization and extinction candidate sub-model sets were identical. When evaluating each model set, the sub-model for the other parameters was set to a null model, in the case of initial occupancy, and a simple time-varying model, in the case of colonization and extinction.

The sub-models were ranked using Akaike’s information criterion (AIC; Burnham and Anderson 2002). The sub-models that were within 2 AIC from the top model were then evaluated in all possible combinations for a final candidate model set of 70 models (using two sub-models for initial occupancy, five sub-models for colonization, and seven sub-models for extinction). Models within 4 AIC from the top model were considered to have some support and those within 2 AIC had substantial support (Burnham and Anderson 2004). Dormann et al. (2018) indicated that removing unsuitable models from the prediction set is a substantial benefit for prediction error; therefore, we calculated and present the model-averaged results of models within 2 AIC of the top model to help with interpretation of the models carrying the most AIC support. We note, however, that when coefficients were model-averaged across all candidate models, results and inferences are qualitatively similar to those presented here (A. Huysman, unpublished data). The models were built on a logit scale, meaning the presented coefficients are log-odds ratios unless otherwise noted (Kéry and Chandler 2016).

**Results**

The proportion of occupied nest boxes increased over the study period, from 30.9% \( (n = 85) \) in 2015 to 32.0% \( (n = 44) \) in 2016, 40.7% \( (n = 52) \) in 2017, and 50.9% \( (n = 138) \) in 2018. The increase in occupancy was dynamic, meaning that while some nest boxes became unoccupied, a greater proportion of boxes were occupied each year. Occupancy and colonization increased, while extinction remained relatively stable over the course of the study (Fig. 2). Of all occupied boxes that were monitored for four years, the mean number of years a box was occupied was 2.5 ± 1.2 \( (n = 84) \). Twenty-seven nest boxes that were occupied for the first time in 2018 were within 2.81 km of a burned area.

The effects of the amount of land cover type around a box and box characteristics generally followed patterns suggested by prior research (Wendt and Johnson 2017), with similar covariates associated with initial occupancy and colonization, and some of those same covariates showing opposing associations with extinction. The sub-model for initial occupancy was the same for 10 out of 12 models within 2 \( \Delta \text{AIC} \), with all models including the amount of grassland, oak savannah, and forest land cover, box height, and box material (wood or plastic) for initial occupancy (Table 2). Two models also included...
Fig. 2. Estimated values of Ψ for each year of the study and γ and ε for each transition period between study years with 95% confidence intervals. Parameters were estimated using multi-season occupancy model with lowest AIC score and mean yearly values of all covariates in model.

The sub-model for colonization was the same for nine out of 12 models within 2 ΔAIC (Table 2). All colonization sub-models included amount of grassland, oak savannah, and forest land cover, box height, box material, year, and amount of fire edge. Two models additionally included the amount of riparian land cover and another
The model included amount of area burned. The sub-model for extinction had seven variations in the 12 models within 2 \( \Delta \text{AIC} \) (Table 2). The sub-model including the amount of grassland, oak savannah, and forest land cover, box height, box material, and year was within this set three times. Other models included the amount of vineyard and riparian land cover, entrance direction, fire severity edge, amount of fire edge, and amount of area burned.

The model-averaged coefficients for nest box and habitat predictors generally showed the same trends across initial occupancy, colonization, and extinction. For both initial occupancy and colonization, the coefficient estimates with 95% confidence intervals that did not overlap zero included amount of grassland (positive), forest (negative), and plastic and wood box material (negative; Fig. 3). The odds ratio of wood over plastic was 4.7 for initial occupancy and 4.9 for colonization. Initial occupancy additionally included height (positive), and colonization included transition years 2016–2017 and 2017–2018 (positive) and amount of fire edge (positive). The only coefficient with a confidence interval that did not overlap zero for extinction was the amount of vineyard (negative; Fig. 3). The effects of the amount of grassland, forest

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**Table 2. Model selection table for multi-season occupancy model.**

| \( \Delta \text{AIC} \) | wAIC | K | Vin | Grs | Oak | For | Rip | Unc | Mat | Dir | Ht | Fir | Edg | Sev | Dist | Yr |
|-------------------------|------|---|-----|-----|-----|-----|-----|-----|-----|-----|----|-----|-----|-----|------|---|
| 0.000                   | 0.063| 24| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 0.296                   | 0.054| 24| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 0.563                   | 0.047| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 0.943                   | 0.039| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.207                   | 0.034| 27| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.498                   | 0.030| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.682                   | 0.027| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.793                   | 0.026| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.844                   | 0.025| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.973                   | 0.023| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.977                   | 0.023| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |
| 1.996                   | 0.023| 25| \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) | \( \Psi \) |

Notes: Symbols for initial occupancy (\( \Psi \)), colonization (\( \gamma \)), and extinction (\( \epsilon \)) indicate whether each variable was included in the sub-model for that parameter. All fire variables were included in the models as an interaction with year. Only models with a \( \Delta \text{AIC} \) between approximately zero and two are presented here. For all 70 candidate models, see Appendix S2. For full column heading names, see notes below table. Variable abbreviations are Vin, vineyard; Grs, grassland; Oak, oak savannah; For, forest; Rip, riparian; Unc, uncultivated; Mat, box material; Dir, entrance direction; Ht, box height; Fir, amount burned; Edg, outer fire edge; Sev, fire severity edge; Dist, distance to fire edge; and Yr, year. Lowest AIC: 728.4.
Fig. 3. Model-averaged coefficient estimates and 95% confidence intervals for multi-season occupancy models within 2 ΔAIC of top model.
land cover, and box material were the opposite of those for occupancy and colonization, but confidence intervals overlapped zero. Riparian, amount of area burned, and box orientation had marginal effects, with confidence intervals overlapping zero for all sub-models in which they appeared.

Wildfire predictors generally had a positive effect on nest box use. Amount of fire edge had a positive effect on colonization of nest boxes between 2017 and 2018, and the confidence interval did not overlap zero (Fig. 3). Outer fire edge had the opposite effect on extinction, but confidence intervals overlapped zero for both. Edge between low severity fire and high severity fire had a negative relationship with extinction and the confidence interval again overlapped zero (Fig. 3).

**DISCUSSION**

Landscape composition can affect the delivery of ecosystem services in agroecosystems (Tscharntke et al. 2005, Lindell et al. 2018), and uncultivated habitat is hypothesized to both enhance the delivery of pest control (Boesing et al. 2017) and increase susceptibility to wildfires (Westerling et al. 2006). In this study, we found that uncultivated habitats near wine grape vineyards elevated the occupancy of nest boxes erected to attract a mobile pest predator. The data also revealed that wildfire, which mainly affected uncultivated habitats, increased nest box colonization. This study provides evidence that fire was positive in the short term for nest box occupancy, which is a desired result from a pest control and management perspective.

Through the course of this study, nest box occupancy increased from 30% to 50%, with some nest boxes consistently occupied, while others experienced local colonization and extinction. The mechanisms and nest box characteristics behind colonization, extinction, and persistence (the probability of a box remaining occupied) underlie the ability of barn owls to nest in vineyards and provide meaningful pest control. With remaining uncertainty over the ability of barn owls to control rodent damage (Labuschagne et al. 2016, Kross and Baldwin 2016, Johnson et al. 2018), a first step for managing their potential for this ecosystem service is confirming our understanding of their nesting preferences both with and without disturbance.

Among the most broad and durable results for management is the finding that open uncultivated land cover types and box material and height had consistent effects on initial occupancy, colonization, and extinction. These results are consistent with those of Wendt and Johnson (2017), who concluded that boxes with uncultivated land nearby, and those that are wooden, at least 3 m high, and facing away from the sun are the most likely to be occupied in Napa Valley. Similar conclusions have also been found in barn owls using nest boxes in Israel (Charter et al. 2010, 2012). Here, we found that barn owls were most likely to colonize and persist in nest boxes with abundant grassland and little forest nearby. The percent of oak savannah and riparian land cover types had marginal effects compared with grassland and forest. The importance of uncultivated land on nest box occupancy and persistence suggests that farm conservation should prioritize the habitats that most benefit barn owls, especially grasslands. Previous studies have also found that barn owls tend to choose breeding sites away from roads, likely to avoid disturbance (Martinez and Zuberogoitia 2004, Frey et al. 2011, Charter et al. 2012). Future work should model changing landscape composition, as well as the effects of habitat loss and restoration on occupancy rates. Barn owl habitat preferences and literature on the positive relationship between landscape heterogeneity and ecosystem services (Tscharntke et al. 2005, Lindell et al. 2018) suggest that changing landscape composition can have significant effects on pest control provided by barn owls.

If we assume nest site selection is adaptive, which is likely given that nest success and survival are important deterministic components of lifetime reproductive success and thus individual fitness, the characteristics associated with increased occupancy should confer some survival or reproductive advantages (Johnson and Wood 2018). Reproduction is likely affected by prey availability, which is probably reflected in land cover variables. Specifically, Botta’s pocket gophers (Thomomys bottae) and California voles (Microtus californicus), important pest species and
prey of barn owls, are most likely to be found in grassland and can reach high densities in this land cover type (Huntly and Inouye 1988, Fehmi and Bartolome 2002, Ordeñana et al. 2012). Nestling survival may be affected by nest box material, direction, and other factors that influence temperature (Charter et al. 2010, 2017, Bank et al. 2019). Future work should examine whether reproductive success is associated with the land cover and nest box variables we have found to affect occupancy and persistence.

The conclusion that barn owls are associated with uncultivated land because that is where rodents thrive introduces a potential trade-off in terms of the services and disservices of uncultivated land. Literature on rodent populations shows that landscape heterogeneity increases small mammal abundance in agricultural landscapes (Fischer et al. 2011), suggesting that land cover types such as grassland could be acting as a source for rodent pests to colonize vineyards (Tscharntke et al. 2016). Though this means that barn owls are more likely to occupy nest boxes near uncultivated land, if rodent densities are high enough in vineyards surrounded by preferred rodent habitat, the conservation of this land cover type could be less preferable for wine producers than vineyards that are far away from uncultivated land where they do not have occupied nest boxes, but they also have fewer rodent pest problems. However, this argument assumes that uncultivated land has no other value besides its relationship with rodent pests. In a survey of 30 Napa Valley wine producers, landowners indicated they left an average of 43% (± 30.5) of their land uncultivated (B. Estes and M. Johnson, unpublished data) and >60% strongly agree that barn owls are helping to control rodent pests (Wendt and Johnson 2017). Though the uncultivated land is in most cases arable, Napa Valley residents choose to conserve (Napa Green 2019) and the local government regulates the amount of land cultivated (Napa County Conservation Development and Planning Department 2005) due to other ecosystem services such as watershed protection (Hannah et al. 2013) and cultural reasons such as the value of terroir, or the importance of the surrounding environment in winemaking (Hira and Swartz 2014). Thus, there are several incentives for Napa Valley wine producers to conserve uncultivated land, which benefits barn owls and, perhaps, pest control.

In addition to the effects of land cover and box characteristics, there were clear signs that fire played a positive role on nest box use between 2017 and 2018. Fire was positively associated with colonization and had an uncertain, though slightly negative, relationship with extinction, and fire variables were in all of the top models. These modeling results align with an observable redistribution of occupied nest boxes the year after the fires. Based on the areas that were newly colonized in 2018, it is likely that the fires altered the habitat in a way that made rodents more available and hunting more accessible. Fire opened canopy in forested areas that made it more similar to the open grasslands and agricultural areas in which barn owls are adapted to hunt (Taylor 1994). In theory, green-up after a wildfire should also be positive for rodent populations, which heavily use recently burned edges (Haim and Izhaki 1994, Schwilk and Keeley 1998, Parkins et al. 2018), but we were not able to measure these mechanisms. The response of barn owls to landscape heterogeneity induced by wildfires is consistent with their response to heterogeneity in non-fire years, when owls are associated with greater availability of diverse uncultivated habitats (Wendt and Johnson 2017).

While the effects of fire, land cover, and nest box predictors had consistent effects on initial occupancy and colonization, the effects of these variables were much more uncertain on extinction. It is noteworthy that the only variable in the extinction model with a confidence interval that did not overlap zero was the amount of vineyard land cover. The reason behind this could be related to nest success, which our dataset did not include. The literature suggests that barn owls are more likely to remain faithful to their mate and to persist (the complement of extinction) in nest boxes when their nesting attempt has been successful (Dreiss and Roulin 2014). Thus, a negative effect of vineyard on extinction could arise if there is a relationship between amount of vineyard and nest success, which should be an area of future research. Additionally, the sub-models for extinction within 2 ΔAIC were overall much more variable than those for initial occupancy and colonization. There was not a clear effect of fire nor nest box and site characteristics besides
vineyard on extinction, suggesting that our set of predictors did not fully capture the mechanisms behind extinction dynamics. Thus, it seems that fire edge had a strong effect on the likelihood of a box being colonized, but fire variables had less of an effect on nest box persistence and extinction. In addition to examination of nest success, future research should investigate the effects of variation in rodent availability in space and time (Klok and De Roos 2007), and weather (Charter et al. 2017) on the likelihood that barn owls persist at individual nest boxes. This work will have direct application, informing whether vineyard managers can maintain high levels of occupancy on their vineyards after initial colonization.

The percent of boxes occupied after fire and modeling results provide evidence that fire was positive in the short term for barn owl nesting, which is a desired result from a pest control and management perspective. However, this is only meaningful for vineyard managers if the owls also remove rodents from their properties. Previous research indicates that about one third of the hunting by vineyard-nesting barn owls occurs within vineyards (Castaneda 2018), which suggests these owls will remove rodents from vineyards, but additional research is needed to determine how many rodents may be removed and whether this removal is economically meaningful. Additional complexity in measuring the effect of barn owls on rodent populations arises because of the landscape of fear in which the presence of predators may cause behavioral changes in prey that result in decreased crop damage by rodents (Brown and Kotler 2004). Until there is more information on how many rodents there are, where they are located, and what areas barn owls remove them from, these results suggest that barn owls were at least able to take advantage of rodent populations that likely increased after fire. This could have helped dampen any rodent damage from increased populations after fire, though a more complete understanding of the role of barn owls in pest control will become clear with increased monitoring of barn owls and rodents in agroecosystems.

Barn owl nest box use is dynamic in nature, but this study revealed that there are characteristics consistently associated with occupancy even after a severe disturbance event. Vineyard managers can make use of these results to decide on the most effective nest box design choices and placement of nest boxes. More work is needed to determine whether the short-term positive effect of fire on occupancy will persist long term, and whether nest box occupancy is a useful indicator of pest control potential.

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Author contributions: Allison E. Huysman and Matthew D. Johnson formulated the questions; Allison E. Huysman collected data and supervised research; Allison E. Huysman and Matthew D. Johnson analyzed the data; and Allison E. Huysman and Matthew D. Johnson wrote the paper.

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