EFFECTS OF LANDSCAPE CONFIGURATION METRICS ON AMERICAN BARN OWL NEST BOX OCCUPANCY AND HUNTING

By

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ABSTRACT

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Harnessing ecosystem services, broadly defined as the benefits nature gives to people, is one approach to minimize the widespread negative impacts of agriculture on wildlife and biodiversity conservation. Conservation biological control is one such service that aims to use natural enemies to reduce crops losses from pests without the use of harmful pesticides, including rodenticides. In Napa Valley, California, human-made nest boxes are deployed on winegrape vineyards to attract barn owls (*Tyto furcata*) that depredate and remove thousands of rodent pests throughout the nesting season. However, the provisioning of this ecosystem service depends on whether a box is occupied and where on the landscape the owls are hunting. In this thesis, I used predictive occupancy models to show that barn owls prefer to occupy nest boxes surrounded by high proportions of grassland, and they prefer to hunt near their nest boxes, near oak savanna habitat, and in areas with a low habitat aggregation. A map of these models combined shows the hunting pressure by the owls in the study site's vineyards. By mapping the provisioning of ecosystem services, landowners can be better informed on how land cover and nest box deployment affect the provisioning of rodent pest removal in their vineyard agroecosystems.

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The research conducted in the Napa Valley study system for the Johnson Habitat Ecology Lab is a collaborative effort spanning multiple years. Various field technicians and fellow graduate students aided with the data collection and analysis found in this research. Likewise, most published scientific papers in ecology are multi-authored, and

some journals now include sections where author contributions are articulated. Therefore, I briefly summarize their contributions and my contributions below. To better reflect the collaborative work of this thesis, I use the plural first person “we” in portions of the Methods where multiple contributors were involved, and I use “I” elsewhere in the document to denote where the work was done by me in consultation with others.

Project Idea and Development: Samantha Chavez, under guidance of Dr. Matt Johnson. Data Collection: Samantha Chavez, Laura Echávez, Jaime Carlino, Dr. Matt Johnson, Asha Moore, Eliana Palomares, Claire Shields, and Aaron Spiller. Data Analyses (Updating the Predictive Occupancy Model): Samantha Chavez and Jaime Carlino. Data Analyses (Adding Configuration Metrics to Occupancy Model, Updating Resource Selection Function, Com): Samantha Chavez. Writing: Samantha Chavez, with editorial contributions by Dr. Matt Johnson and committee members Drs. Ho Yi Wan and Micaela Szykman Gunther.

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INTRODUCTION

Modern agriculture has allowed human civilization to flourish by increasing food production and security, but often at the cost of impacts to global biodiversity (Tilman et al. 2011, Tscharntke et al. 2012, Ortiz et al. 2021). Global demand for crop production is projected to rise over the coming half century due to both the increasing human population and per capita rate of consumption, putting additional strain on native habitats and biodiversity (Tilman et al. 2011, Balmford et al. 2012, Ortiz et al. 2021). Maximizing sustainable crop yields can help meet this demand while reducing the need for agricultural land expansion, which can in turn mitigate the impacts of agriculture on biodiversity (Baulcombe et al. 2009, Tilman et al. 2011, Balmford et al. 2012, Tscharntke et al. 2012, Garnett et al. 2013). Maintaining high crop yields requires minimizing losses to pests, so pest management is vital for the future of sustainable agriculture (Hatfield et al. 2011, Bommarco et al. 2013, Baldwin et al. 2014). Chemical pesticides are economically costly and pose significant threats to human health and non-target wildlife species (Pimentel 2005, Sharma et al. 2020). In contrast, conservation biological control seeks to contribute to pest suppression by supporting populations of natural enemies (Begg et al. 2017). Harnessing natural enemies for pest removal can help maintain yields while supporting biodiversity within an agroecosystem (Green et al. 2005, Power 2010). Conservation biological control is an example of a regulating ecosystem service, defined as a benefit nature provides to people by moderating a natural phenomenon (Daily 1997).

One widespread example of conservation biological control is the implementation of barn owl (*Tyto alba* and *Tyto furcata*) nest boxes to attract rodent-eating owls to agricultural fields. Controlling rodent pests has been a challenge for farmers since the dawn of agriculture and is increasingly important in ensuring food security globally (Stenseth et al. 2003, Brown et al. 2007). Barn owl nest boxes are used in many regions of the world including in Malaysian rice fields (Hafidzi and Mohd 2003), Israeli crop fields such as alfalfa and date plantations (Charter et al. 2009, Meyrom et al. 2009, Kan et al. 2014), and in the winegrape vineyards of Napa Valley, California (Wendt and Johnson 2017). Previous research has shown that owls hunt in Napa Valley vineyards (Castañeda et al. 2021), remove thousands of rodents from the landscape (St. George and Johnson 2021), and can meaningfully reduce gopher activity (Browning et al. 2016, Hansen and Johnson 2022), which reduce yield. The owls also heavily use and may be partially reliant on nearby preserved native habitat, such as riparian habitats and grasslands (Wendt and Johnson 2017, Castañeda et al. 2021, Huysman and Johnson 2021*a*). Thus, protecting native habitats and deploying owl nest boxes could provide a form of conservation biological control that benefits farmers and biodiversity alike.

Quantifying ecosystem services can help communicate the value of biodiversity in ways that reflect dominant political and economic views (Wenny et al. 2011, Johnson and Hackett 2016), and mapping ecosystem services can clarify to landowners how landscapes affect the provisioning of services across space (Burkhard and Maes 2017). Specifically, closer examination of the relationships between owls and habitats could potentially incentivize conservation of native habitats in agricultural landscapes that could help conserve biodiversity and facilitate rodent removal. Pest removal services are dependent on the dispersion of natural enemies across a landscape, and therefore the composition and configuration of habitats in a landscape can influence the delivery of ecosystem services, especially for highly mobile predators (Power 2010, Burkhard and Maes 2017). While composition refers to the amounts and different types of landcover classes in a landscape, configuration refers to how these landcover types are arranged (McGarigal and Marks 1995). One such configuration metric is the arrangement of habitat edges which have been commonly shown to drive wildlife behaviors and ecological processes (Lidicker 1999, Pfeifer et al. 2017). Previous studies have noted that predators may be attracted to edges in an agricultural landscape due to the presence of prey (Šálek et al. 2010). Habitat configurations in heterogeneous landscapes such as Napa could strongly affect hunting by barn owls, which have been shown to use edges for hunting (Andries et al. 1994, Bond et al. 2005). Earlier work has examined how the composition of habitats affect barn owl nest box occupancy and hunting habitat selection (Wendt and Johnson 2017, Huysman and Johnson 2021*a*), but the role of habitat configuration is unresolved. By modeling the effect of both landscape composition and configuration on the selection of nest boxes and hunting habitat by barn owls, we can create a visual and spatially explicit representation of the pest removal services barn owls are providing on vineyards in Napa Valley.

Here, we build on previous work by testing the hypothesis that including metrics of landscape configuration that we hope will improve previously developed models for nest box occupancy (Wendt and Johnson 2017, Huysman and Johnson 2021*a*) and hunting habitat selection (Castañeda et al. 2021, Huysman and Johnson 2021*b*). We then combine the updated nest box occupancy and hunting habitat selection models into a single spatially explicit model to visually depict hunting pressure by the owls in the study system. This research contributes to agroecology by revealing the effects of uncultivated habitats on the provisioning of an ecosystem service in cropland (Power 2010, Pywell et al. 2015).

IACUC

This study was conducted under Cal Poly Humboldt IACUC #2021W12.

Study System

The study site (Figure 1) was in the Napa Valley in Napa County, California, which encompasses several cities from south to north including American Canyon, Napa, Yountville, St. Helena, and Calistoga. Napa County is characterized by a Mediterranean climate with wet, cold winters and dry, hot summers (Swinchatt et al. 2004). It is located about 112 km north of San Francisco, California and the valley is bounded by the Mayacamas Mountains on the west and the Vaca Range on the east (Swinchatt et al. 2004). The valley is flat and grassy in the south near San Pablo Bay and extends 80 km northwards growing narrower and more forested. The county is known for its diversity of microclimates and soils (Swinchatt et al. 2004), as well as its heterogenous landscape of agricultural fields (majority wine grape vineyards), and variously sized grasslands, oak savannas, forests, and riparian areas.

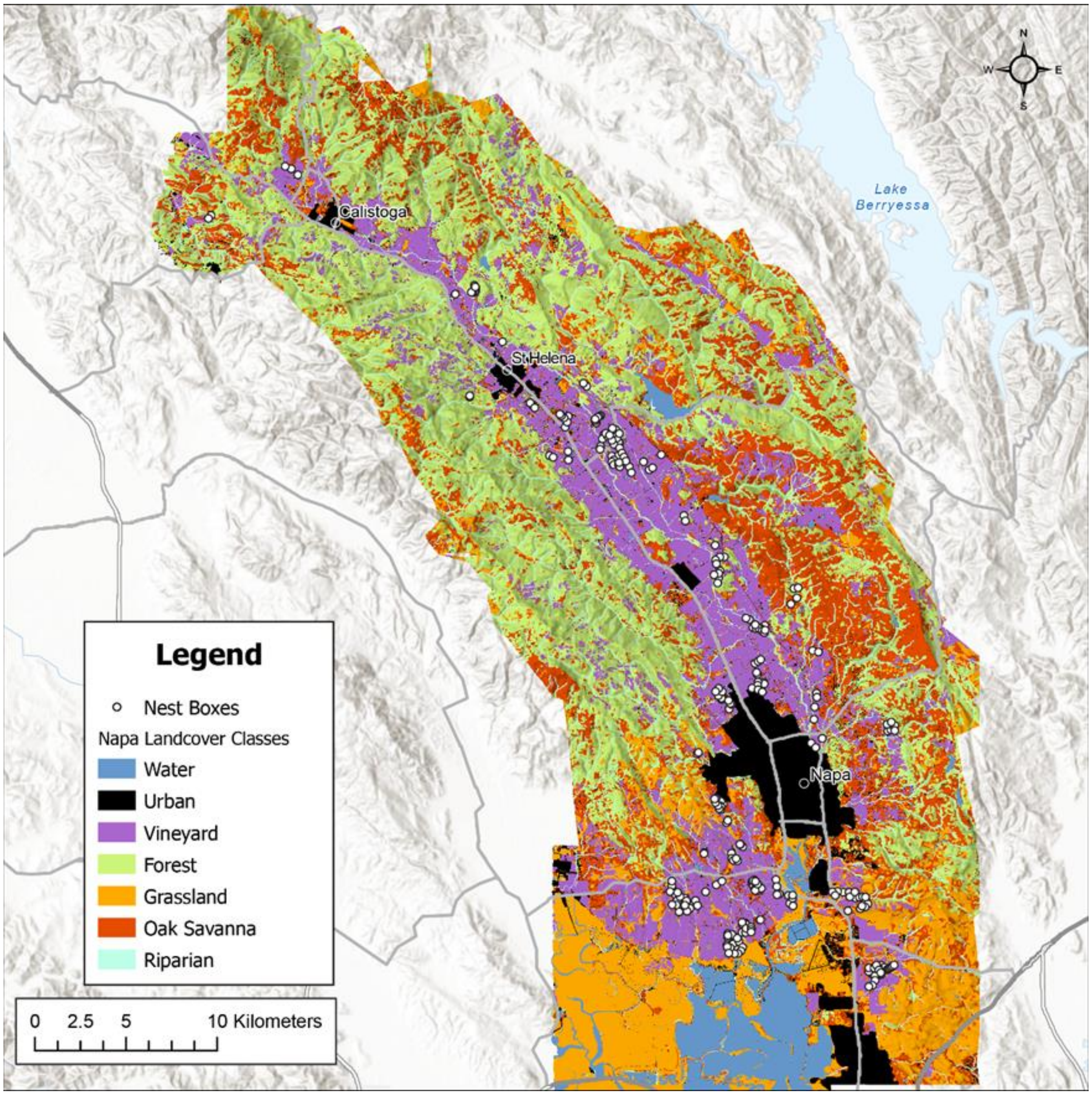

Figure 1: Study area with Napa Valley landcover raster used in analysis. Seven land cover classes are included and described in detail in Corro (2021). The urban land cover class was created from Corro's land cover class of 'other'. White points are the nest box locations of the 288 nest boxes monitored in 2021. Southern Napa is characterized by the grassland and water land cover classes, while the mountains on the east and west of the valley are a combination of heavily intermixed forest and oak savanna classes. The thin lines of the riparian class are throughout the map. The valley itself is heavily classified as mostly vineyard or urban, though vineyards to extend into the south. Base map source: ESRI, NASA, NGA, USGS, County of Napa, California State Parks, HERE, Garmin, SafeGraph, FAO, METI/NASA, BLM, EPA, NPS

Barn owls (*Tyto* spp.) are found globally, except in Antarctica (Roulin 2020). In California, the American Barn Owl (*Tyto furcata*) is a voracious predator of crop-damaging rodents including gophers, moles, voles, and mice (Kross et al. 2016). Over a year, an average family of barn owls in Napa Valley (2 adults and 3.6 nestlings) is estimated to kill over 3,400 rodents (St. George and Johnson 2021). Barn owls are cavity nesters, and readily occupy nest boxes once deployed. These mobile predators are not territorial, and many pairs of barn owls will nest in boxes with other occupied nest boxes nearby (Roulin 2020). This makes the barn owl an excellent candidate for providing rodent pest removal (Kross and Baldwin 2016, Kross et al. 2016, Roulin 2020)

Barn owls can have large home ranges, with foraging males going as far as 5.6 km from the nest to hunt (Roulin 2020). For barn owls in Napa's heterogeneous landscapes, these home ranges will usually encompass winegrape vineyards, field margins, and a range of native habitats, making this an excellent study system for investigating effects of habitat composition and configuration on ecological processes.

METHODS

This research involved four core steps. First, we updated previously conducted owl nest box occupancy models with nest box attributes, local habitat, and landscape composition as predictors, making use of more years of data and higher resolution GIS layers. Second, I tested the hypothesis that including habitat configuration metrics as additional predictor variables improved these occupancy models. Third, I similarly tested whether the addition of habitat configuration variables improved a previously published model of owl hunting habitat selection based on GPS telemetry. Fourth, I combined the top models to create a spatially explicit model of predicted owl hunting pressure based on the distribution of monitored nest boxes in the valley, the likelihood of their occupancy, and the owls' patterns of hunting habitat selection.

Updating the Occupancy Model

The first part of our analysis sought to update an earlier predictive model for barn owl nest box occupancy measured in 2015 and 2016 in winegrape vineyards (Wendt and Johnson 2017) by using a higher resolution raster dataset (4 by 4 meter spatial resolution vs 30 meter pixels) of the land cover of Napa Valley, including landscape configuration metrics, optimizing the scale of selected covariates, and training the model with six years of occupancy data (2015-2020). We define occupancy as the presence of eggs or chicks in a nest box during at least one nest box check throughout the reproductive season of March through July. Nest boxes were visually inspected for occupancy using a GoPro®

camera mounted on an extendable painter's pole to stream a live feed of the inside of a nest box to the nest box monitor's phone. While the schedule of nest box checks varied throughout the years 2015 to 2021 in both timing and number of boxes checked, generally the checks were once a month across the breeding season, with 3-4 checks of every box. Modeling of detection probability has confirmed that with our techniques the probability of missing reproductive occupancy after 3 monthly checks was 4.9% and after 4 monthly checks was 1.85% (Carlino et al. unpubl. data). These very low probabilities of missed occupancy also are unlikely to be affected by the variables hypothesized to affect occupancy (e.g., nest box or habitat), so little is gained by parameterizing detection probability in our modeling; thus, we consider our data as providing estimates of true reproductive presence (1) and absence (0) at each nest box each year. We used generalized linear models (GLMs) with a logit link function to model nest box occupancy (0/1) as the response variable, and we used various combinations of predictor variables to build candidate model sets, which we describe below, and assessed models with Akaike's Information Criterion corrected for small sample size, AICc. All continuous covariates were first standardized with a mean of zero for analysis, and we assessed multicollinearity by constructing correlation matrices and removing predictors with $r \geq |0.7|$. Based on earlier modeling (Wendt and Johnson 2017, Huysman and Johnson 2021*a*), we included a quadratic form for the grassland predictor variable, and we included only additive effects. We evaluated our models by training our model on occupancy data from 2015 to 2020 and then tested it against data from 2021. More specifically, we report the percent correct classification (PCC), Kappa, and the True Skill

Statistic (TSS) using thresholds that maximize each of their values, and the area under the Receivers Operating Characteristic (AUC) as a threshold-independent measure of the top model's predictive performance (Fielding and Bell 1997, Allouche et al. 2006).

We conceptualized predictor variables hypothesized to affect barn owl nest box occupancy in three 'levels': nest box attributes, local landcover conditions, and landscape landcover composition and configuration. The box attributes included box height, pole height, box material (W or P for wooden or plastic, respectively), entrance hole orientation (cardinal direction), box area (floor space), and hole diameter. Previous work suggested other variables (such as box volume, presence of a perch, heat shield, or interior partition) did not strongly affect occupancy (Wendt and Johnson 2017), so they were excluded from analysis to limit the number of predictors. Local landcover condition included the proportion of 7 landcover classes (water, vineyard, urban, grassland, riparian, oak savanna, and mixed forest; see Appendix A for full descriptions), which we examined at 5 different radii around the nest box to reflect the immediate surroundings of a nest site (20, 50, 75, and 100 m around a nest box). The landscape level covariates included the proportion of the same land cover types within 10 larger radii around each box (500, 750, 1000, 1250, 1500, 1750, 2000, 2250, 2500 and 2810 m). These radii were selected to reflect barn owl hunting distances around nest boxes in this system as described by Castañeda et al. (2021) who found that 50% of hunting took place within 500 m of the nest box, 73% of hunting took place within 1 km of the nest box, and that the mean maximum hunting range was 2.81 km. We included both local and a landscape level scale in our modeling because we hypothesized that owls could respond to habitat differently very near the nest box (e.g., affecting the nest site's exposure to shade, predators, etc.) and at home range scale (e.g., preferred hunting habitat). To optimize scales at both the local and landscape levels, we evaluated each covariate separately with a univariate GLM at each radius, then used AICc to select the single best scale for each covariate, and then combined the covariates (at the optimized univariate scale) into a single multi-variable, multi-scale model (i.e., method "ms5" in (McGarigal et al. 2016). All landcover proportions were extracted from a 4x4-m spatial resolution land cover raster of Napa Valley (projection NAD83 UTM Zone 10N) created by Lucila Corro (2021) and used in a previous analysis of nest box occupancy (Huysman and Johnson 2021*a*). This raster is an improvement in spatial resolution compared to the raster used in Wendt and Johnson 2017 which used the USDA CropScape 30 by 30 meter spatial resolution raster of Napa Valley. All statistical analyses were conducted using R (R Core Team 2022).

Once the scales of both local and landscape predictors were optimized, we reduced the total number of predictor variables to include in a candidate model set by using univariate GLMs for each covariate and removing from further consideration those that explained relatively little of the deviance in occupancy (< 6%). The final pool of predictor variables included three box attributes (pole height, box height, and box material), two predictors at the local level (grassland and forest cover at a 150 m radius), and two predictors at the landscape level (forest and grassland cover at a radius of 2810 m). These predictors were combined in logical sets to examine whether nest box occupancy was best predicted by one of more of each of the hypothesized levels, including box attributes only, box attributes and local level predictors, and so on up to a "saturated model" containing all predictors at all three levels. To this candidate model set we also added a null model (intercept only), as well as the top model from previous publications (Wendt model and Huysman model from Wendt and Johnson [2017] and Huysman and Johnson [2021*a*], respectively). Only models that were within a delta AIC of 2 were considered competitive and averaged (Arnold 2010). A predictive map of the model projected across Napa Valley was created in R using the following equation,

$$w(x) = \frac{\exp(\beta_0 + \beta_1 X_1 + \cdots \beta_k X_k)}{1 + \exp(\beta_0 + \beta_1 X_1 + \cdots \beta_k X_k)}$$

and utilized binary rasters for each covariate (X) and coefficients (β) produced by the model. For mapping purposes, the rasters representing nest box attributes were set to common preferred values (i.e., 24 in box, 12 foot pole; see Results).

Adding Landscape Configuration Metrics to the Occupancy Model

After updating the occupancy model as described above, we then tested the hypothesis that the inclusion of landscape configuration metrics would improve the model. To quantify landscape configuration, we used the configuration metrics functions in R package *landscapemetrics* (Hesselbarth et al. 2019) and rasters of the landcover types in Napa Valley to measure the values of each metric at radii around the nest boxes. These metrics included the interspersion and juxtaposition index (IJI) of all land cover types at each nest box at the class level (each landcover type separately) and at the landscape level (across all landcover types). The IJI describes the intermixing of classes and higher values are found when patches of one type of landcover are equally adjacent to all other landcover types (McGarigal and Marks 1995). We also quantified edge density at the class level for each of the seven landcover types, mean patch size at the class level, and contagion at the landscape level, which measures the extent to which landcover types are aggregated or clumped. We obtained the values for each landscape metric at the same radii as the landscape level radii described above (500-2810 m around the nest box), and again applied the same scale optimization procedure, removal of collinear predictors ($r \geq |0.7|$), and removal of uninformative predictors (here, deviance explained < 5%) as described above. Many of the configuration covariates were dropped due to low deviance explained or correlations with each other or with landscape composition metrics already included in the updated occupancy model (Appendix B), yielding only two landscape configuration predictors to add to the candidate model set: class level IJI values for grassland at a 2810 m radius around the nest box and the edge density values for oak savanna at a radius of 2500 m around the nest box. Finally, three models were created and compared using AICc: the updated occupancy model from step one, the same model with the inclusion of the configuration metrics, and a model that only included box level covariates and the configuration metrics.

Adding Landscape Configuration Metrics to a Hunting Habitat Selection Model

I also aimed to determine if the inclusion of landscape configuration metrics could improve a model of hunting habitat selection by Castañeda et al. (2021), which was a Resource Selection Function (RSF, Davis et al. 1994) built from 260 used hunting locations obtained from each of 11 female barn owls fitted with Uria 300 Global Positioning Systems (GPS) tracking units (Gdynia, Poland) contrasting with the same number of available locations randomly drawn from within each tagged owl's home range (95% minimum convex polygons). The owls' movements were tracked with telemetry and the transmitter recorded locations of the owls once per minute. The top model in Castañeda et al.'s (2021) resource selection function included the additive effects of land cover type, distance to nest box, and distance to the oak savanna land cover class.

I selected three landscape configuration metrics to add to candidate models, each measured at 25, 50, and 100 m radii around each used and available point analyzed by Castañeda et al. (2021): aggregation index (an index for how many pixels in a radius share edges of the same land cover type) (He et al. 2000), edge density at the forest class level, and edge density at the landscape level. I chose the aggregation index for this analysis rather than the contagion index used in the occupancy model because the former works better with smaller radii relevant for point-based analyses such as RSFs. I chose to emphasize the forest at the class level because barn owls are hypothesized to sometimes hunt along forest edges (Séchaud et al. 2021) and because of the previous apparent contradiction that barn owls in Napa Valley avoided nesting in boxes with abundant forest nearby (based on occupancy modeling of Wendt and Johnson [2017] and Huysman and Johnson [2021a]) but showed positive selection for forest when hunting (based on hunting telemetry analysis of Castañeda et al. [2021]). As above, I used scale optimization to univariately analyze and determine the best scale for each configuration metric and all were found to perform best at 25 m radius of used and available points. I added these landscape configuration metrics as covariates to Casteñeda's top model and created several RSF models with various combinations of the covariates. All models also included the individual owl as a random effect. Then I compared the AICc scores of the models to find if landscape configuration metrics would improve the previous top model. The top model's performance was evaluated as per (Boyce et al. 2002), which involves calculating the predicted probability of use for every point (used and available), dividing them into 10 equal bins, and regressing the mean predicted probability of use in each bin against the proportion of used locations in each bin. A model with strong predictive probability should have a Pearson's correlation coefficient close to one and a positive slope significantly different than zero.

As with the predictive occupancy map, the same steps were completed to create the predictive hunting habitat selection map. Rasters for distance to box and distance to oak savanna were created using the Euclidean Distance raster tool in ArcGIS Pro (Esri Inc. 2021). Due to the size of the file, the Napa Valley landcover raster was tiled in ArcGISPro then processed using FRAGSTATS software (McGarigal and Marks 1995) to generate rasters of the landscape configuration metrics before being mosaicked back together in ArcGISPro.

Combining Maps to Create the Ecosystem Services Provisioning Map

The fourth and last step of my analysis involved combining the top occupancy and hunting habitat selection models from the previous steps into a spatially explicit predictive map. Using package *rgeos* (Bivand and Rundel 2023) and *terra* (Hijmans 2023) from the R programming language, Euclidean distances to nest box rasters were created for each individual nest box in our study site and applied to a loop that created resource selection functions utilizing the distance to nest box raster of a single nest box. This was done for each box active in 2021 for which there was a predicted occupancy output from the occupancy model, for a total of 288 resource selection function rasters following the hunting habitat selection model equation. Each nest box's resource selection raster was multiplied by the corresponding predicted occupancy value from the nest box occupancy model, yielding a raster depicting the probability an owl from a given box would hunt in a pixel, weighted by the occupancy probability of that box. These 288 rasters were then added together in R using the raster package and rescaled, so that values ranged from zero to one. This approach models the dispersion of predicted owl hunting from the actual nest boxes used in our study, accounting for the distribution nest boxes, their probability of occupancy, and patterns of hunting habitat selection. However, it is important to note that while the 288 nest boxes in this model are representative of those in Napa Valley, we do not monitor all nest boxes in the Valley; there are at least dozens of additional unmonitored boxes in the Valley that are not a part of our study. The hunting pressure in our composite map is therefore underestimated in areas with nest boxes that we do not monitor. Thus, the resulting map from this work is most meaningfully interpreted at the scale of individual vineyards, where all boxes in the projected extent are monitored.

RESULTS

The top updated nest box occupancy model, prior to the addition of configuration metrics, was the full or saturated model, which included all covariates at the box, local, and landscape levels (Table 1). No other models were within 2 AICc and the top model carried 99% of the model weight in the candidate set. The top model showed barn owl occupancy was positively associated with pole height, box height, and wooden boxes (

Table *2*). Barn owls also preferred boxes with higher proportions of grassland at the 150 m (local) and 2,810 m (landscape) scales. We found a negative relationship between forest land cover around the nest box at both the local (150 m) and landscape levels (2,810 m). Of the covariates in the model, only grassland at the 150 m radius and forest at the 2,810 m radius had confidence intervals that overlapped zero, meaning they had weak effects within the model. Notably, grassland land cover and oak savanna land cover at the landscape scale were correlated, so there is likely a positive relationship with both grassland and oak savanna. This model performed well; when the model based on training data from 2015-2020 was tested against occupancy data from 2021, the PCC was 75.3%, the Kappa was 0.485, the TSS was 0.478, and the area under the ROC curve was 0.84. Adding landscape configuration metrics did not significantly improve the model. Its ΔAICc was >2 and the saturated model without configuration metrics carried 88% of the model weight in the candidate model set (

Table 3). The saturated model was used to develop a map predicting the probability of nest box occupancy by barn owls (Figure 2).

Table 1. The candidate model set for the updated barn owl predictive occupancy model for nest boxes in Napa Valley, CA 2015-2020, showing the number of parameters (k), AICc, ΔAICc, and model weight (w). This set of models did not include landscape configuration metrics. Grassland 2810 m was set in the model as an orthogonal polynomial.

Model Name	**k**	**Covariates**	**AICc**	**ΔAICc**	***w***
saturated.model	9	Pole Ht, Box Ht, Box Material, Forest 150 m, Forest 2810 m, Grassland 150 m, Grassland 2810 m	742.84	0	0.99
box.landscape	7	Pole Ht, Box Ht, Box Material, Forest 2810 m, Grassland 2810 m	763.97	21.12	< 0.01
Huysman.model	6	Pole Ht, Box Material, Forest 2810 m, Grassland 2810 m	819.43	76.59	< 0.01
box.local	6	Pole Ht, Box Ht, Box Material, Forest 150 m, Grassland 150 m	823.23	80.39	< 0.01
Wendt.model	10	Pole Ht, Entrance Category, Box Material, Riparian 2000 m, Forest 2810 m, Grassland 150 m, Grassland 2810 m	824.31	81.47	< 0.01
local.landscape	6	Forest 150 m, Forest 2810 m, Grassland 150 m, Grassland 2810 m	889.56	146.71	< 0.01
landscape.level	4	Forest 2810 m, Grassland 2810 m.	908.30	165.47	< 0.01
box.level	4	Pole Ht., Box Ht., Box Material	988.85	246.01	< 0.01
local.level	3	Forest 150 m., Grassland 150 m.	1057.79	314.95	< 0.01
null.model	1	1	1258.17	515.32	< 0.01

Table 2. The coefficients in the top predictive occupancy model for barn owl nest boxes in Napa Valley, CA, 2015-2020. The covariates, estimates with standard errors, and confidence limits are listed. Grassland at the landscape level appears twice as it was set as an orthogonal polynomial in the model.

Covariate	**Estimate ± SE**	**Lower CL**	**Upper CL**
Intercept (Box Material Plastic)	-1.43 ± 0.26	-1.95	-0.94
Pole height (ft.)	0.29 ± 0.08	0.14	0.47
Box height (in.)	0.60 ± 0.08	0.43	0.76
Box Material Wooden	1.00 ± 0.28	0.48	1.57
Forest – Local	-0.54 ± 0.13	-0.77	-0.28
Grassland – Local	0.06 ± 0.09	-0.10	0.24
Forest – Landscape	-0.18 ± 0.11	-0.41	0.02
Grassland – Landscape	10.53 ± 1.82	6.98	14.12
Grassland – Landscape^2	-4.29 ± 1.27	-6.85	-1.84

Table 3. Candidate model set for nest barn owl nest box occupancy, with and without the addition of landscape configuration metrics showing the number of parameters (k), AICc, ΔAICc, and model weight (w). The saturated model was the full model that was the top model from Table 1.

Model	**k**	**Covariates**	**AICc**	**ΔAICc**	***w***
Saturated model	9	Pole Height, Box Height, Box Material, Local Level Forest, Local Level Grassland, Landscape Level Forest, Landscape Level Grassland	742.84	0	0.88
Saturated Model with Configuration Metrics	11	Pole Height, Box Height, Box Material, Local Level Forest, Local Level Grassland, Landscape Level Forest, Landscape Level Grassland, Grassland IJI, Oak Savanna Edge Density	746.86	4.02	0.12
Composition Metrics replaced with Configuration Metrics	9	Pole Height, Box Height, Box Material, Vineyard Edge Density, Grassland Edge Density, Oak Savanna Edge Density, Grassland IJI, Water IJI	758.49	15.65	0.00

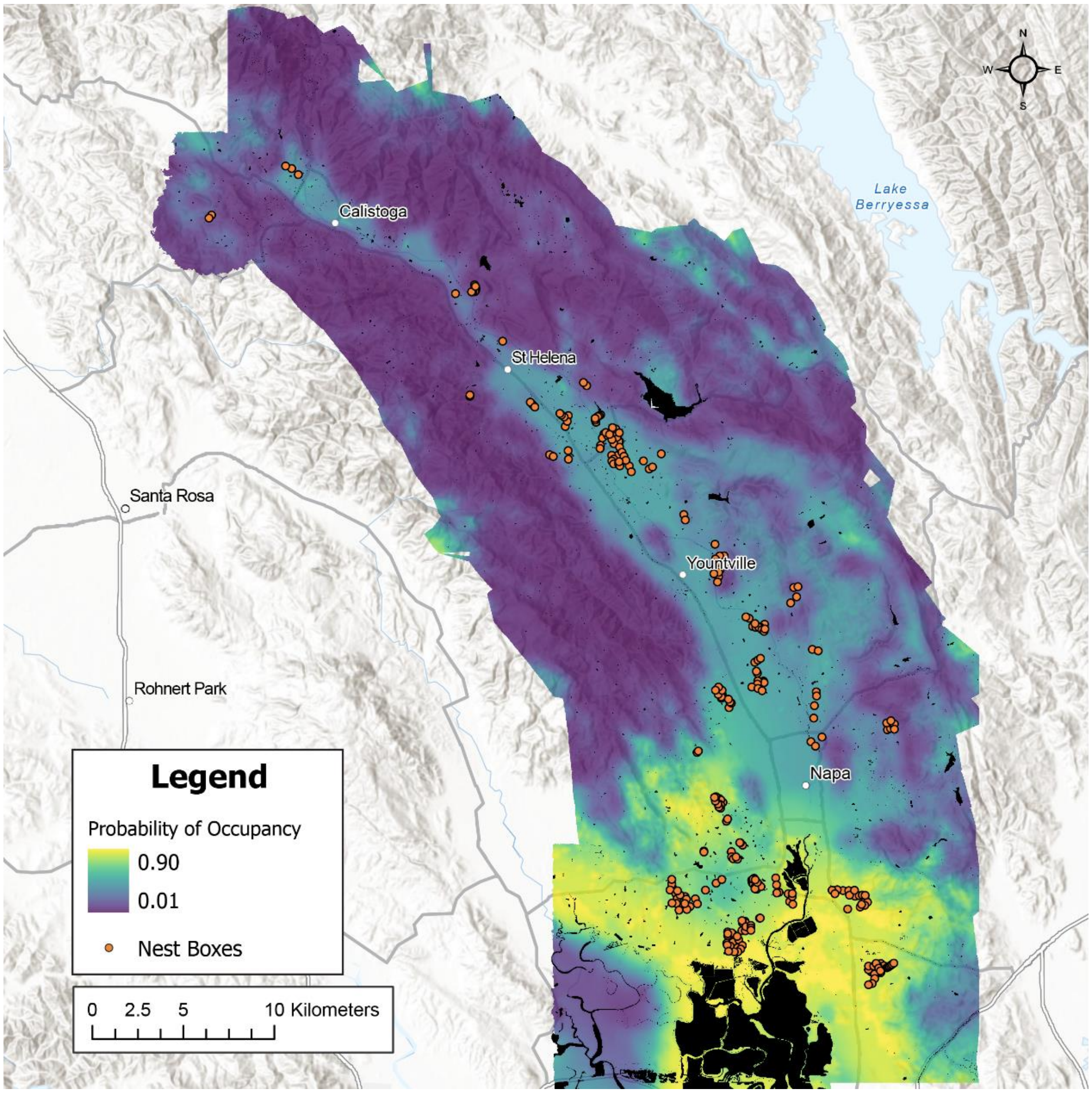

Figure 2. The predictive map for probability of nest box occupancy by barn owls in Napa County, CA based on data from 2015-2020. The orange points are the monitored nest boxes in our study. The water land cover class was added in black, as nest boxes cannot be placed in open water. This map was based on a model that did not incorporate grassland as a polynomial. Base map source: ESRI, NASA, NGA, USGS, County of Napa, California State Parks, HERE, Garmin, SafeGraph, FAO, METI/NASA, BLM, EPA, NPS.

In contrast to the occupancy model, landscape configuration metrics improved the fit of the hunting habitat selection model. The top three models in our candidate set included configuration metrics, and the original hunting habitat model from Castañeda et al. (2021) without configuration metrics, was ranked fourth (

Table *4*). The top two models were competitive, with ΔAICc < 2, and they included forest class edge density, landscape edge density, and aggregation index along with habitat category, distance to box, and distance to oak savannah habitat, as found in Castañeda et al. (2021). I model-averaged the two top performing models weighted by AIC (Burnham and Anderson 2002) to calculate coefficients of the model, as the primary goal was to create a predictive map (Arnold 2010). Model-averaged coefficients suggested a strong preference for hunting in areas with less aggregated land cover classes, and weak but positive relationships with forest edge density and landscape edge density (Table 5). As with the older model, there were strong negative effects of distance to nest box and distance to oak savanna. The categorical landcover covariate, called 'habitat' in this model, had different influences on hunting habitat selection depending on the category, but the trends were generally the same as in the previous model created by Castañeda et al. (2021), with owls showing preference for hunting in riparian and savanna habitats, and they used urban, vineyard, and water land cover classes proportionally less than their availability. Our model evaluation via resubstitution indicated that our averaged top model was a strong predictor of used location points. The linear relationship between the mean predicted probabilities and the proportion of use within each bin yielded a Pearson's correlation coefficient of 0.973, and the slope of the regression line was significantly different than zero ($F_{1,10}$= 143.5, $P < 0.005$) and an adjusted R^2 of 0.95. The averaged model was projected across the Napa Valley landscape (Figure 3) to visually communicate where owls from our study site are hunting the most.

Lastly, combining the top occupancy model, the top hunting habitat selection model, and the distribution of monitored nest boxes in our study revealed a map of predicted hunting pressure by barn owls on the landscape that is focused primarily on the southern portion of the valley where nest box density and occupancy rates are highest and favorable habitat is abundant (**Error! Reference source not found.**). The map is most meaningfully interpreted at the scale of individual vineyards. For example, vineyards with low numbers of nest boxes and little preferred habitat show very low hunting pressure (Figure 4A), whereas vineyards with large numbers of high-occupancy boxes and abundant preferred native habitats nearby show high hunting pressure (Figure 4B). In between are vineyards with large numbers of boxes but relatively little native habitat (Figure 4C), and vineyards with substantial native habitat but comparatively few nest boxes (Figure 4D).

Table 4. Candidate model set for hunting habitat selection showing the number of parameters (k), AICc, ΔAICc, and model weight (w). Each model included a random effect based on individual owls, denoted by (1|id) in the model covariates column. Covariates named Dbox represents distance to nest box, habitat is the categorical covariate for the landcover in which owls were hunting in, Dsav represent distance to oak savanna habitat on the landscape, AggIndex represents the aggregation index, ForestED represents forest edge density, and LandscapeED represents edge density of the landscape. Models are numbered inconsecutively because our model selection table included models run by Castañeda et al. (2021).

Model	**Model Covariates**	**k**	**AICc**	**ΔAICc**	***w***
m7	Habitat, Dbox, Dsav, AggIndex25, (1|id)	11	6922.59	0	0.67
m2	Habitat, Dbox, Dsav, ForestED25, LandscapeED25, AggIndex25, (1|id)	13	6924.12	1.53	0.31
m5	Habitat, Dbox, Dsav, ForestED25, (1|id)	11	6932.57	9.98	0.00
m1	Habitat, Dbox, Dsav, (1|id)	10	6932.94	10.35	0.00
m6	Habitat, Dbox, Dsav, LandscapeED25, (1|id)	11	6933.16	10.57	0.00
m4	Dbox, ForestED25, LandscapeED25, AggIndex25, (1|id)	6	7471.60	549.01	0.00
m3	ForestED25, LandscapeED25, AggIndex25, (1|id)	5	7815.96	893.37	0.00
Null model	1, (1|id)	2	7933.61	1011.02	0.00

Table 5. The model-averaged coefficients of the competitive hunting habitat selection models from Table 4 (models 2 and 7), both of which included landscape configuration metrics.

Coefficient	**Estimate ± SE**	**Lower CI**	**Upper CI**
Intercept (Habitat: Forest)	3.69 ± 0.67	2.37	5.01
Habitat: Grassland	-0.07 ± 0.19	-0.45	0.31
Habitat: Riparian	0.48 ± 0.22	0.04	0.91
Habitat: Savanna	0.35 ± 0.19	-0.03	0.73
Habitat: Urban	-1.30 ± 0.27	-1.84	-0.77
Habitat: Vineyard	-1.12 ± 0.18	-1.48	-0.76
Habitat: Water	-2.85 ± 0.33	-3.49	-2.20
Distance to Box (DBox)	-4.03 ± 0.23	-4.48	-3.58
Distance to Oak Savanna (Dsav)	-0.52 ± 0.23	-0.97	-0.08
Aggregation Index (AggIndex25)	-2.30 ± 0.66	-3.61	-1.00
Forest Edge Density (ForestED25)	0.49 ± 0.43	-0.35	1.33
Landscape Edge Density (LandscapeED25)	0.15 ± 0.24	-0.32	0.62

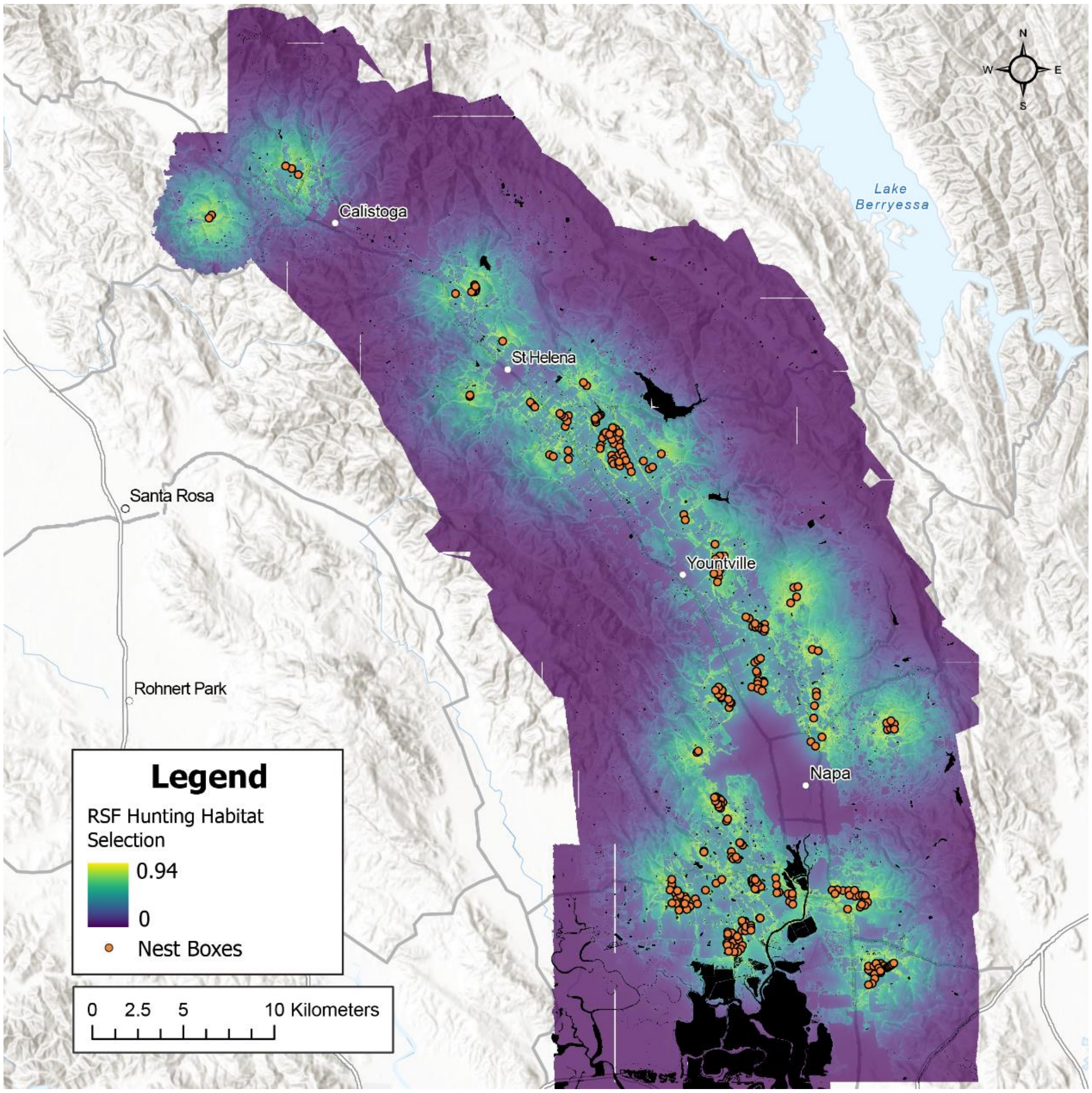

Figure 3. The resource selection function map for hunting habitat selection by barn owls in Napa County, CA under the existing distribution of nest boxes and based on occupancy data from 2015-2020. Base map source: ESRI, NASA, NGA, USGS, County of Napa, California State Parks, HERE, Garmin, SafeGraph, FAO, METI/NASA, BLM, EPA, NPS.

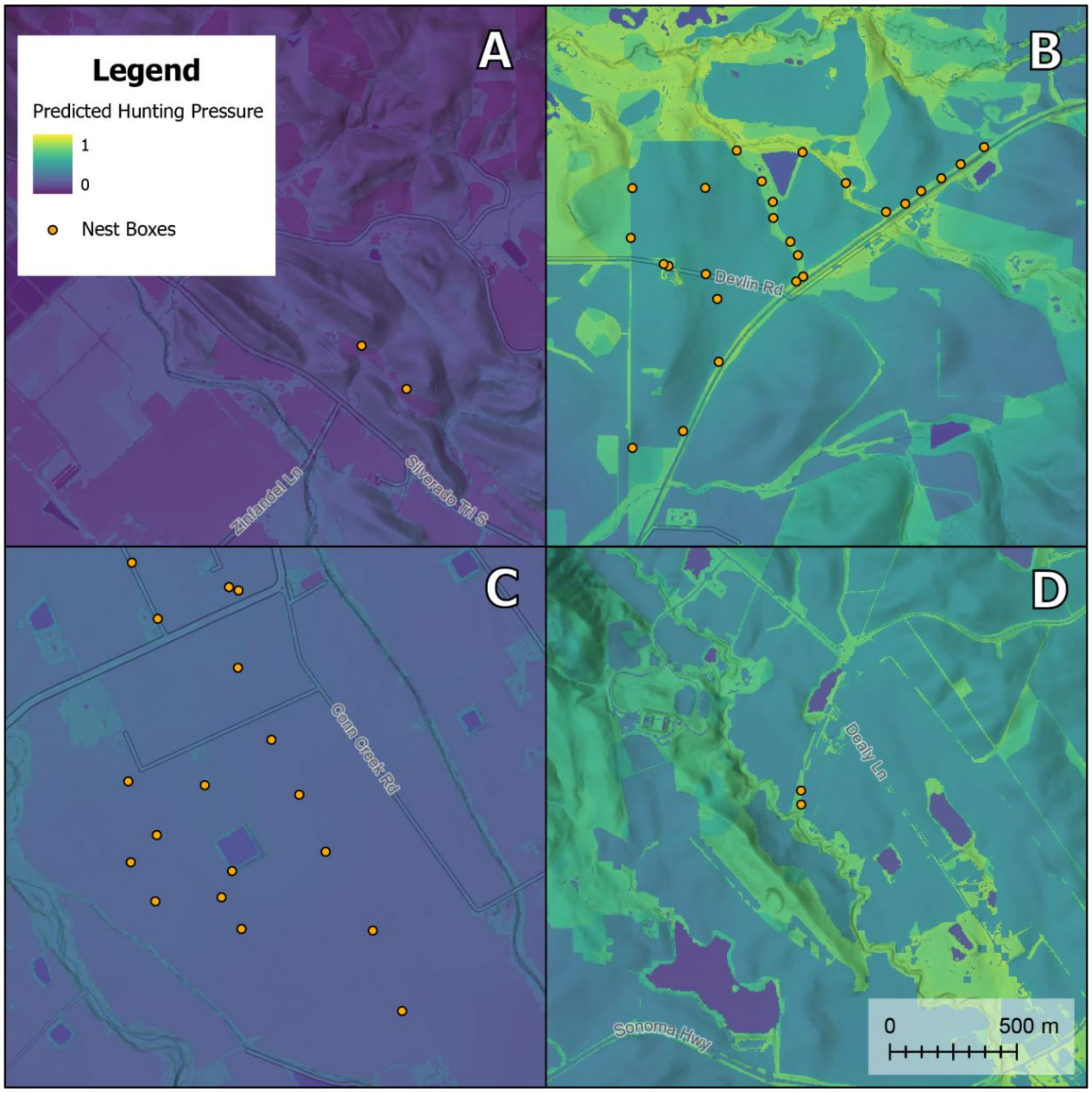

Figure 4. Predicted owl hunting pressure based on the distribution of existing nest boxes, their probabilities of occupancy, and the owls' habitat preferences in Napa County, CA based on data from 2015 – 2020. Here, several vineyards with nest boxes were focused on at a scale of 1:24,000. In box A, a vineyard with few boxes is surrounded by relatively little preferred landcover. Box B shows a vineyard with many nest boxes surrounded by abundant preferred landcover, while box C shows a vineyard with many nest boxes surrounded by less preferred hunting landcover classes. Finally, Box D shows a vineyard with very few boxes but with abundant preferred landcover. The preferred land cover classes were grassland, oak savanna, and riparian. Base map source: ESRI, NASA, NGA, USGS, County of Napa, California State Parks, HERE, Garmin, SafeGraph, FAO, METI/NASA, BLM, EPA, NPS.

DISCUSSION

Mapping ecosystem services is a vital step in both understanding how landscapes affect their delivery (de Groot et al. 2010, Wu 2013, Rega et al. 2018) and communicating to landowners the importance of landscape composition and configuration for the provisioning of valuable services, such as vertebrate pest removal by barn owls for farmers. Mapping the ecosystem services of barn owls may be of interest to farmers because the use of barn owls has been found to be economically beneficial (Kan et al. 2014). Here, I combined an updated model of barn owl nest box occupancy with a multi-scale model of hunting habitat selection improved by the inclusion of landscape configuration metrics to create a spatially explicit model of hunting pressure by a vertebrate predator of economically damaging rodent pests. These results suggest that at the scale of the Napa Valley region, the barn owls in our study system are providing pest removal services heavily in the southern end of Napa Valley (Figures 1 and 2). At the scale of the individual vineyard, the distribution of boxes, their likelihood of occupancy, and the owls' preferences for hunting combine to create strong differences in the amount of pressure hunting owls are expected to exert within and near vineyards (Figure 3). Information on the impacts of land use practices on ecosystem services production is essential for landowners to optimize their system for conservation biological control (de Groot 2010). Furthermore, the information provided by mapping ecosystem services can even be used to inform policy making to optimize provisioning of ecosystem services (Maes et al. 2012, Rega et al. 2018, Bruskotter et al. 2019). There has been tremendous progress in mapping ecosystem services to inform conservation action (Burkhard et al. 2013, Burkhard and Maes 2017), but relatively few studies have mapped biological pest removal (Malinga et al. 2015), and this study is among the first to do so for vertebrates (but see Civantos et al. 2012).

Our results suggest that habitat configuration metrics matter both for owl hunting behavior and for more accurately mapping ecosystem service delivery. In our system, owls showed a preference to hunt in areas with a low habitat aggregation, that is areas with many landcover classes intermixed, and to a lesser extent in places with high edge density. Previous research into barn owl behavior has indicated that there is some preference for hunting along wildflower strips, meadow-like fields, and forest edges (Séchaud et al. 2021), perhaps because of concentrations of prey in these areas coupled with the owls' adaptations for relatively open environments. This preference for hunting in areas with high edge density has been found in other raptor species and study areas as well, such as in the hen harrier (*Circus cyaneus)* in Scottish moorlands (Arroyo et al. 2009). However, in our study system, nest box occupancy was not strongly associated with landscape configuration metrics but was well-predicted by nest box attributes and local and landscape-level habitat composition, as previously reported (Huysman and Johnson 2021*a*). It is not yet clear why the owls' preference of edges and low habitat aggregation for hunting did not also correspond with a preference to occupy nest in boxes with these attributes nearby. One possibility is that nest box selection is shaped by a balance of preferences not just for hunting habitat, but also for cover, safety from predators (i.e, great-horned owls, *Bubu virginianus*) and other factors, which could dampen preferences for conditions that favor hunting specifically. Indeed, habitat selection is a complex behavior that can vary, and barn owls are not the only species to display variability in habitat selection under various circumstances (Roever et al. 2014, McMahon et al. 2017, Picardi et al. 2022). Barn owl habitat selection can depend on whether the bird is hunting, selecting a roost, or commuting (Séchaud et al. 2021). While landscape composition and configuration seem similar, and indeed several of our individual metrics of them were correlated, our results indicate that both concepts should be considered when studying habitat selection, as metrics that may be important for one component of owl behavior may not matter as much for another. The weaker effect of the local level landscape composition of forest and grassland in the occupancy model seems to show that the use of barn owl nest boxes will be more successful when implemented in a region with preferred occupancy landcover as opposed to trying to find a specific location in a vineyard. Landowners can decide on nest box placements away from forest and nearer grassland on their property, but overall having a vineyard in a region with lots of grassland will have a greater impact on nest box occupancy. The negative effects of the forest land cover class at the local level shows that barn owls do not tolerate well having a nest box near forest land cover class, though this negative effect is weaker than the overall positive effect of placing nest boxes in a region with lots of grassland as evidenced by the strong positive effects of grassland at the landscape level.

Some important caveats to the work done here include the scope of our project and our collected data. First, while our list of potential predictor variables for nest box occupancy and hunting habitat was long and included factors operating at various levels and spatial scales, I was unable to include vineyard management practices, which vary in both space and time. Previous work (Wendt and Johnson 2017) suggested that nest box occupancy did not vary among organic and conventional vineyards, but other vineyard management practices could affect owls. In Napa Valley, virtually all vineyards use cover crops, but their composition varies from a standard mix of planted species selected to promote soil fertility (such as oats [*Avena sp*.], barley [*Hordeum sp*.], common vetch [*Vicia sativa*], fava beans [*Vicia faba*], daikon radish [*Raphanus sativus*], and field mustard [*Brassica rapa*]), to a feral mix of species common in the environment (especially field mustard, European annual grasses, and storksbill [*Erodium cicutarium*]). In addition, the vines themselves are of various ages and managers use several trellising methods, and these differences affect the physical structure of the habitat and/or the local rodent populations in ways that could impact owls' selection of nest boxes or areas for hunting. Future research should examine the effect of cover crops and vine age and structure on the owls hunting habitat selection. While our work shows the owls use the vineyards less than expected given their commonness in the study area, vineyards are still heavily used, with approximately one thirds of hunting locations occurring within them (Castañeda et al. 2021).

Second, our map of owl hunting pressure only took into consideration the boxes we were able to monitor within the study site and is therefore best interpreted at extents of individual vineyards. Nonetheless, these individual vineyard maps can be useful for pinpointing areas in the study site where good quality habitat and high probability of occupancy coexist at a vineyard where few nest boxes are currently deployed. These vineyards could be said to be underutilizing nest boxes and would benefit from deploying more boxes (e.g., Figure 3D). Other areas on the map reveal vineyards that are unlikely to benefit much from using owl boxes, due to poor local and landscape level habitat and low probabilities of occupancy (e.g., Figure 3A). These landowners would be advised against adding more nest boxes, as the probability of occupancy would still be low in the area. Vineyards with high rates of occupancy, suitable surrounding habitat, and intense hunting pressure may seem as if they have 'maxed out' the number of boxes in their system, but because barn owls readily occupy nest boxes even near other barn owls, additional boxes could still provide additional pest removal. Indeed, they could even expand beyond the current cluster of nest boxes on their land and continue to add boxes in more remote corners of their property, or perhaps even encourage their neighbors to begin deploying nest boxes as well.

A logical next step for this research is to test the effects of hypothetical land use actions with simulations. For example, where are the optimal places to deploy new boxes to maximize the increase in predicted owl hunting pressure? Also, how is owl hunting pressure affected by the addition and distribution of nest boxes, and how is this mediated by local native habitat? How is it affected by the loss or addition (restoration) of native habitat? The barn owls' preference for low aggregation index landscapes points to a preference for habitat patches that are not large and contiguous. This lends support to the idea that the restoration or creation of strips of preferred habitat to hunt may increase ecosystem services, much in the same way that (Séchaud et al. 2021) found that wildflower strips were greatly preferred in Europe. Thus, perhaps the inclusion of relatively inexpensive linear features, such as tree lines and hedgerows, may serve to reconfigure habitats in ways that substantially increase the hunting pressure imposed by owls on vineyards. Previous studies using simulations of landscapes have uncovered how landscape changes can affect provisioning services (Nelson et al. 2009, Railsback and Johnson 2014). Simulating restoration of native habitats such as riparian zones or grassland patches throughout the valley could model the effects of restoration on bolstering provisioning services. Overall, the impact of this research is in providing a spatially explicit model and map of ecosystem services provided by a highly mobile predator in an agroecosystem, and future work should investigate how these services can be affected both by land use and the deployment of more nest boxes.

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APPENDIX

Appendix A: A table with the land cover classifications that apply to the 4 by 4 meter spatial resolution raster (NAD 83 UTM ZONE 10N) created and described by Corro (2021). This raster was used in this analysis as well as in the study by Huysman and Johnson (2021*a*), wherein the land cover class 'other' was renamed as Urban and pixels in city or urban boundaries were reclassified as urban.

Name of Land Cover Class	**Definition**
Water	"…an area where water is the primary and persistent land cover type."
Oak savanna, or Oak dominant savanna	Classified by a tree canopy of 10-75% tree canopy cover, "…suggests that oak savanna exists where both grassland and sparse tree canopy cover are present"
Forest, or forested land cover	"…land covered by vegetation with heights of 1 meter or greater and a total canopy cover of greater than 75%."
Grassland	"…vegetative land cover with canopy heights of less than 1 meter."
Vineyard	"…agricultural land dedicated to viticulture."
Riparian	"…areas that are within 30 meters of a river or stream, and where forest or oak dominant savanna is present."
Urban, classified as Other in Corro (2021).	"…land cover that does not exhibit any of the above characteristics was classified as other and is considered to include land cover that is urban, developed, or bare ground."

Appendix B: A table showing the covariate selection process for the landscape configuration metrics. Only the metrics within the top ten of percent deviance explained (PDE) values are included in this table as the others were dropped immediately. Correlation shows the value of correlation and the metric it was correlated with. If a metric was correlated with another in the top ten for percent deviance explained, they were decided between by whichever metric had a higher percent deviance explained. This narrowed down the 23 metrics to just five (in bold) of which only oak savanna edge density and grassland IJI were included into the analysis.

Configuration Metric	Correlation	PDE
Vineyard Edge Density	Contagion (0.7) and Vineyard Composition Landscape Level (0.8)	13.69
Forest Edge Density	Grassland Edge Density (-0.8) and Vineyard Mean Patch Size (-0.8)	26.52
Grassland Edge Density	Grassland Composition Landscape Level (0.9) and Oak Savanna Local Level (0.9)	35.01
Oak Savanna Edge Density	None	5.06
Contagion	Vineyard Edge Density (0.7)	10.93
Water IJI	Grassland Composition Landscape Level (-0.7)	13.46
Grassland IJI	None	15.29
Vineyard Mean Patch Size	Forest Edge Density (-0.8), Grassland Edge Density (0.7), Water Mean Patch Size (0.7)	13.57
Water Mean Patch Size	Water Edge Density (0.8) and Vineyard Mean Patch Size (0.7)	6.33
Grassland Mean Patch Size	Grassland Edge Density (0.7)	28.47

Appendix C: The map for probability of nest box occupancy and hunting habitat selection by barn owls in Napa Valley, CA based on data from 2015 – 2020. This map depicts predicted owl hunting pressure based on the distribution of existing nest boxes, their probabilities of occupancy, and the owls' habitat preferences. High nest box density, rates of occupancy, and occurrence of suitable habitat likely contribute to the higher rates of hunting in the south than in the north. Base map source: ESRI, NASA, NGA, USGS, County of Napa, California State Parks, HERE, Garmin, SafeGraph, FAO, METI/NASA/ BLM, EPA, NPS.