

Forecasting the effect of land-use change on native and non-native mammalian predator distributions

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Abstract. Intensive land use can fragment continuous natural areas into smaller patches, which may be too small to support viable populations of native fauna and more susceptible to invasion by alien species. We demonstrate the utility of combining species occurrence models with land-use change models to identify areas where future development may differentially affect wildlife. Occurrence data for native (e.g., gray fox, coyote, bobcat, mountain lion, striped skunk, raccoon) and non-native (e.g., domestic dogs, domestic cats, opossums) mammalian predators were collected from 188 remotely triggered camera locations across an oak woodland and vineyard landscape in northern California. The occurrence data were used in combination with landscape variables extracted using a geographic information system to build explanatory models of predator occurrence. These statistical models were used to derive two surfaces showing relative probability of occurrence for non-native and native predators. Then, a spatially explicit land-use change model was used to examine potential future predator distributions given potential future vineyard expansion. The probability distribution models generated hypothesized low probabilities of occurrence for native predators within large vineyard blocks, but higher probabilities within isolated vineyards and also in oak woodlands. The models suggest the highest probabilities of non-native predator occurrence fell within large blocks of vineyard. Using one possible future vineyard development scenario, the distribution models illustrate areas where probability of native predator occurrence may be reduced and where non-native predators may expand due to vineyard development. This technique could be applied to prioritize acquisition of critical wildlife habitat and maintain habitat connectivity for wildlife populations.

Introduction

Human activities throughout the world are resulting in widespread natural habitat loss and fragmentation that threatens the survival of wildlife (Kucera and Barrett 1995; Bennett 1999). Understanding the effects of this habitat loss and fragmentation is important to conserving biodiversity (Bierregaard Jr. et al. 1997; Wilcove et al. 1998). Many studies have linked fragmentation to deleterious environmental consequences (e.g., Saunders 1990; Bolger et al. 1997; Crooks and Soulé 1999). The biological effects of habitat fragmentation range from a decline in species requiring large amounts of connected natural habitat to displacement of and increased predation on native fauna (Beier

1993; Wiens 1996; Stefan 1999). As a means to diminish negative consequences of human-induced habitat fragmentation and to enhance connectivity of populations across landscapes, conservation biologists have proposed the maintenance of natural habitat corridors (Forman 1995; Bennett 1999; Perault and Lomolino 2000).

Until recently, most habitat fragmentation research focused on natural areas and corridors, but increasingly researchers are recognizing that modified land may not be uninhabitable by all species. As such, conservation biologists have recently focused more attention on examining biodiversity within modified lands in addition to monitoring natural areas (McIntyre and Hobbs 1991; Hanski and Simberloff 1997; Ricketts et al. 2001). Altered habitat may affect species differently; it may slow, enhance, or neutrally impact the movement of species (Duelli et al. 1990), and species unable to use modified land may be more prone to extinction (Gascon et al. 1999; Bentley et al. 2000).

Some native species may move through modified landscapes surrounding core habitat areas, which together is referred to as the 'matrix'. (Laurance 1991), finding and utilizing remnant natural habitat patches (Lindenmayer et al. 1999). However, wildlife use of modified lands may depend on the landscape configuration of these areas and size of the remaining natural habitat (Aberg et al. 1995; Dunn 2000). For example, wolves in northern Italy were most active in agricultural land adjacent to forested areas (Massolo and Meriggi 1998). Depending on the species, distance from natural habitat patches may influence use of human-modified habitat (Downes et al. 1997; Perault and Lomolino 2000). Species may have different scales of response such that some species may be found farther from natural habitat patches than others (Ricketts et al. 2001). Diversity of habitats nearby (Wright and Tanimoto 1998; Drapeau et al. 2000) and structure or cover remaining in the human impacted areas also may affect species presence at a given point in the landscape (Bentley et al. 2000).

Wide-ranging animals found at low-densities, such as carnivores, are often among the first species to go extinct where human activity fragments natural systems (Beier 1993; Primm and Clark 1996; Mac Nally and Bennett 1997). Loss of carnivores can lead to a cascade of effects throughout the system leading to additional loss of species or release of mesopredators (Power et al. 1996; Crooks and Soulé 1999). To avoid this, we need to understand how animals are distributed across the landscape in order to conserve land that will support native carnivores.

Statistical modeling techniques, such as logistic regression analysis (Hosmer and Lemeshow 2000), and geographic information systems (GIS) may be useful in exploring how animals use fragmented systems (e.g., Huhta et al. 2004). Combinations of these tools have been used to examine resource selection and spatial partitioning (Erickson et al. 1998; Massolo and Meriggi 1998; Clark et al. 1999; Johnson et al. 2000; Reunanen et al. 2002), the impact of local vs. landscape variables (Bolger et al. 1997; Drapeau et al. 2000), disease outbreak (Gumpertz et al. 2000), effects of climate (Walker 1990; Zimmermann

and Kienast 1999), and land-use change (Landis and Zhang 1988, 1998; Heaton and Merenlender 2000).

Here we demonstrate the utility of combining species models with land-use change models to identify potential areas of future conflict between development and wildlife. This paper focuses on mammalian predators in the oak woodland and vineyard landscape where predators may be impacted as natural habitat becomes more fragmented by agricultural development. Mammalian predator occurrence data and landscape variables were used to develop explanatory logistic regression models of predator occurrence, which were used to derive surfaces showing relative probability of occurrence for non-native and native predators. Results from a previously developed vineyard expansion model (Heaton and Merenlender 2000) were used to explore potential impacts of future vineyard expansion on predator distributions. The resulting models and probability surfaces can be used to identify regions within the landscape where native species' probability of occurrence is likely to remain high given both current and future conditions and may be useful in highlighting particular parcels where conservation action is needed. Extrapolating the results of the regression analyses across the landscape also serves to establish hypothetical distributions of species that may be tested through further field efforts.

Methods

Study area

Research was conducted in eastern Sonoma County, California, where vineyards are the dominant land use. The land cover types in the area include vineyards, rural residential, rangeland, and natural habitat. In 2002, vineyards covered a reported 59,891 acres (Agricultural Commission 2002) of the 1,000,000 acre county, with most vineyards lying in the drier eastern half of the county. In this region, most valley bottoms are highly modified, having largely been converted from oak woodland and oak savanna to vineyards and residential development. Remnant natural habitat generally occurs along creeks, some of which consists of hardwood dominated riparian vegetation and/or oak woodland/savanna vegetation depending on the location of the creek and amount of natural habitat remaining. Oak forest and woodland is the dominant cover type on the hillsides surrounding the valley bottoms. In recent years, especially during the second half of the 1990s, an increase in global demand for premium wines (e.g., Fairbanks et al. 2004) has fueled rapid expansion of vineyards in coastal California. For example, over 20,000 acres were planted between 1995 and 2002 in Sonoma County alone (Agricultural Commission 2002). This expansion has often been associated with conversion and fragmentation of natural habitat, including hillside woodlands (Merenlender 2000; Fairbanks et al. 2004). Though development has slowed dramatically during

the last few years (Agricultural Commission 2002), new vineyards continue to be planted.

California's oak woodlands provide critical habitat for over 100 bird, 60 mammal, and 80 amphibian and reptile species (Pavlik et al. 1991), so conservation of oak woodland habitat and species is a vital part of maintaining California's biodiversity. Because more than 80% of California's oak woodlands fall under private ownership (Bolsinger 1988; Greenwood et al. 1993), this research was conducted mostly on private and also some public properties in Sonoma County, California (Hilty and Merenlender 2001) (Figure 1).

Occurrence data for mammalian predators were collected at sites situated along the western foothills of the Mayacmas Mountains, spanning approximately 70 km from northern Alexander Valley to southern Sonoma Valley (Figure 1). This region experiences a Mediterranean climate and is primarily covered by mixed oak woodlands, varying in canopy closure from open to dense, with shrub communities at higher elevations. The over-story is predominantly coast live oak (*Quercus agrifolia*), Oregon oak (*Q. garryana*), valley oak (*Q. lobata*), black oak (*Q. kelloggii*), and blue oak (*Q. douglasii*), with a diverse understory of grasses and shrubs. The focal area for modeling represents the approximate region in Sonoma County where true oaks (*Quercus spp.*) dominate the landscape and encompasses 260,247 ha (Figure 1).

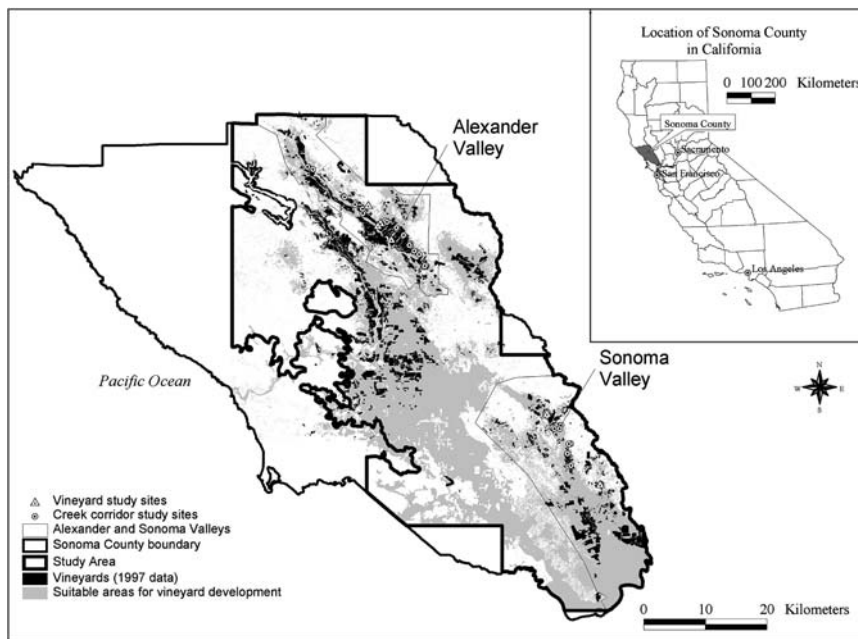


Figure 1. Location of Sonoma County and Alexander and Sonoma Valleys in California. Study area refers to the region dominated by true oaks. Current vineyards and lands predicted to be suitable for vineyard development based on past trends ($p < 0.5$) (Heaton and Merenlender 2000) are illustrated.

Monitoring techniques

Our monitoring stations were originally set up to compare wildlife abundance along valley riparian areas of differing width, and in vineyards at different distances from large patches of natural habitat (Hilty 2001; Hilty and Merenlender 2004). So, camera locations were restricted to creek corridors where detection rates of mammalian predators were high (0.35 ± 0.31 detections/night) and the vineyard matrix where detection rates were lower (0.03 ± 0.01 detections/night) (Hilty and Merenlender 2004). Thus, the available wildlife detection data used to develop these models was from within vineyards and along creeks, the two major landscape components in the region's valley bottoms outside of residential areas. Because of the constraints of the prior field research questions, the camera locations were not randomly selected across the entire landscape or stratified across the disturbance gradient.

The species occurrence data used to develop our models were collected during 1999–2000 from 188 camera locations using non-baited remotely triggered cameras. Camera locations were placed at least 45 m apart and remained in position for 30 functional days (i.e. cameras had film and charged batteries). This was a sufficient length of time to minimize our failure to detect error based on our calculations of the latency to first detection (14.8 days \pm 10) (Hilty 2001; Hilty and Merenlender 2004). This index is based on the average number of sampling days required to obtain evidence of all species detected present at each study area using unbaited cameras (Zielinski and Stauffer 1996). These methods optimized our monitoring effort and reduced the potential for false-negatives in the data set, but failure to detect an animal was not confirmation of the absence of a species, especially over multiple years.

Two predator detection cameras were placed at 21 independent creek corridor sites. At four creek sites, two additional cameras were placed in adjacent vineyards at a distance of 200 m from the vineyard edge/creek corridor as a pilot effort to detect predators in vineyards. Six vineyards then were more thoroughly sampled using 23 remotely triggered cameras distributed in approximately five linear transects to cover each entire vineyard block. Study sites were independent from one another due to the distance and barriers between the sites (Hilty and Merenlender 2004). More details and maps of the camera locations can be found in Hilty and Merenlender (2004). Species detections and home ranges are listed in Table 1.

GIS data

A geographic information system (GIS) (Arc/Info: ESRI, Redlands, California) was used to quantify several landscape variables for each camera location. We quantified amounts of natural habitat and distance to natural resources based on other studies suggesting that such landscape variables may be

Table 1. The number of points out of 188 where mammalian predators were detected by remotely triggered cameras (Hilty 2001), and home range sizes (Crooks 2002). Note that multiple photos were often taken of a single species by a camera, as 564 photos were taken of mammalian predators in total.

Species	Home range (km ²) Average (range)	No. of cameras where detected
Gray fox	0.69 (0.22–1.87)	21
Coyote	5.69 (0.66–11.96)	12
Bobcat	2.94 (0.24–5.63)	12
Mountain lion	492 (112–829)	1
Striped skunk	0.21 (0.11–0.37)	35
Raccoon	0.52 (0.39–0.65)	26
Opossum ^a	0.20 (0.05–2.54)	32
Domestic dog ^a	n/a ^b	6
Domestic cat ^a	0.40 (0.001–3.80)	42
Any native species	n/a	71
Any non-native species	n/a	61

^aNon-native species.

^bDomestic dogs in this study area are largely not feral and not relying on natural resources to survive, instead moving around with and by humans making home range irrelevant.

important (Bolger et al. 1997; Gascon et al. 1999; Ricketts et al. 2001). Three digital land-cover data layers were used to best delineate natural habitat and modified lands in the late 1990s: (1) the California Department of Forestry (CDF) vegetation layer, which is derived from 1990 Landsat satellite imagery (25 m resolution); (2) the California Department of Conservation's Farmland Mapping and Monitoring Program (FMMP) 1998 Important Farmland layer for Sonoma County, which focuses on delineation of farmland from 1:24000 infrared aerial photography; and (3) Circuit Riders Production, Incorporated (CRP) 1997 vineyard location layer, in which vineyards were delineated from 1990 1:24000 aerial photographs that were enlarged and digitized at a 1:6000 scale with input from landowners. Farmland and vineyard vector data were converted (25 m × 25 m resolution) to be compatible for raster analyses in Arc/Info. For each land-cover layer, we classified individual land-cover types as either natural habitat or modified land. Land-cover categorized as modified land included vineyard, farmland, urban, water, and other. A composite layer of modified lands (25 m × 25 m cells) was created by combining the modified land from all three land-cover layers, where remaining areas were classified as natural habitat. Natural habitat included woodland, hardwood, conifer, shrub, and grass. It was categorized broadly because all of the mammalian predators under study are habitat generalists (Hilty and Merenlender 2000).

Because small fragments of natural habitat may not be useful to mammalian predators, core natural habitat was defined and delineated. Our use of the term 'core' habitat refers to large areas of continuous natural habitat. In order to delineate areas of core natural habitat, we modified Saving's (1998) 'core.aml' habitat fragmentation analysis program and applied it to our derived natural

habitat/modified land data layer. Core habitat was defined using the following rules: (1) core natural habitat areas consisted of 1000 ha or more of connected natural habitat. One thousand ha was selected as a threshold value because it captured the large areas we knew to be undeveloped but excluded many small isolated patches that would have been included if we used a smaller threshold value; (2) individual core habitat patches were considered to be connected if they were not separated by more than two 25 m × 25 m pixels (e.g., Saving and Greenwood 2002), and (3) edge habitat was eliminated by removing a one pixel (25 m × 25 m) buffer around each identified patch of core habitat. Non-core natural habitat was then delineated and consisted of both edge habitat and the fragments of natural habitat that did not meet the criteria for core habitat.

Using our derived data layers of natural habitat, core natural habitat, and non-core natural habitat, we determined values for a number of landscape variables. Euclidean distances from each camera location to natural habitat, core habitat, and non-core natural habitat were calculated. Additionally, amount of all natural habitat, core habitat, and non-core natural habitat were calculated for each camera location using 500, 1000, and 2000 m radii. Amount of natural habitat, core natural habitat, and non-core natural habitat also were calculated for a number of annuli (i.e. donuts) including 500–1000 m, 1000–2000 m, and 500–4000 m from each camera location in order to be able to test more specifically if species were responding to different landscape scales that make ecological sense (Table 2). These distances were arbitrarily selected to represent different scales at which species may respond to the landscape.

Table 2. Twenty-two spatially explicit variables tested in initial logistic models.

Variables tested mixed stepwise regressions

Distance to core habitat
 Distance to natural habitat
 Distance to water
 Diversity of habitat within 125 m²
 Diversity of habitat within 500 m²
 Amount of core natural habitat within 500 m
 Amount of core natural habitat within 1000 m
 Amount of core natural habitat within 2000 m
 Amount of all natural habitat within 500 m
 Amount of all natural habitat within 1000 m
 Amount of all natural habitat within 2000 m
 Amount of non-core (fragmented) natural habitat within 500 m
 Amount of non-core (fragmented) natural habitat within 1000 m
 Amount of non-core (fragmented) natural habitat within 2000 m
 Amount of core natural habitat 500–1000 m
 Amount of core natural habitat 1000–2000 m
 Amount of all natural habitat 500–1000 m
 Amount of all natural habitat 1000–2000 m
 Amount of non-core (fragmented) natural habitat 500–1000 m
 Amount of non-core (fragmented) natural habitat 1000–2000 m
 Amount of core natural habitat 500–4000 m
 Amount of all natural habitat 500–4000 m

Other landscape variables were also quantified. Diversity of habitat types near each camera location was assessed using the 1990 CDF hardwood-vegetation layer. Two habitat diversity values were calculated for each camera location – the number of habitats that fell within 125×125 m and the number of habitats within 500×500 m (e.g., Wright and Tanimoto 1998). Each of the 12 habitat classes in the hardwood-vegetation database were treated as a unique habitat type: (1) blue oak woodland, (2) blue oak/gray pine woodland, (3) valley oak woodland, (4) coastal oak woodland, (5) montane hardwood, (6) potential hardwood, (7) conifer, (8) shrub, (9) grass, (10) urban, (11) water, and (12) other. Euclidean distance to nearest stream or body of water was calculated for each camera location using the US Census Bureau 1994 'TIGER/Line' data. A total of 22 landscape variables were generated (Table 2).

Model construction

We used mixed stepwise logistic regression analysis to assess the relative strength of association between quantified landscape variables and the occurrence of native predators and non-native predators. To satisfy the assumptions of logistic regression and because the rate of false-negatives was minimized, the lack of species detection by cameras was treated as an absence. Two best-fit statistical models were generated, one for all native predator species and one for all non-native predator species. These models were then used to create probability surfaces ($25 \text{ m} \times 25 \text{ m}$ cells) that show a hypothesized distribution for native predators and one for non-native predators. All 22 generated variables (Table 2) were evaluated during construction of the statistical models for both the native and non-native predators. In addition, the probability of a native predator being present at a given location (determined by extracting values from the probability surface generated for native species) was included as an additional variable for testing in the non-native model. We did this because other researchers have suggested that native species may limit the distribution of non-native species (e.g., Crooks and Soulé 1999).

The selection process was a forward selection with a backward look between forward steps. The variable with the lowest Wald χ^2 and a $p < 0.25$ was accepted into the model, and only variables with Wald χ^2 probability of $p < 0.05$ were retained in the model. Because the amount of all, core, and non-core habitat within 500, 1000, 2000, and 4000 m radii included overlapping areas, all other variables containing areas of overlap were dropped from the stepwise selection when a variable was incorporated (i.e. statistically significant) in a model. For example, amount of core habitat within 500 m and amount of all natural habitat within 1000 m could not be included in the same model.

The resulting explanatory logistic regression models were then used to generate native and non-native relative probability surface models in the approximate region in Sonoma County where true oaks dominate the landscape. Coefficients from the explanatory best-fit logistic models were used to

calculate a probability value for each cell in the study area such that:

$$\pi = \frac{e^{\beta_0 \beta_1 \chi_1 + \mathbf{K} \beta_n \chi_n}}{1 + e^{\beta_0 \beta_1 \chi_1 + \mathbf{K} \beta_n \chi_n}}$$

For the probability surface for native species, π is the probability that a native predator is present; for the probability surface for the non-native species, π is the probability that a non-native predator is present. In addition, $\beta_0 \dots \beta_n$ are the coefficients and $\chi_1 \dots \chi_n$ are the landscape variables. The resulting probability surfaces show hypothesized distributions of native and non-native mammalian predators across the current landscape (Figures 2 and 3).

In addition to predicting current distributions of mammalian predators, we wanted to examine the effects of future vineyard expansion on distributions. To do this, we used an existing vineyard-expansion model that was developed for Sonoma County (Heaton and Merenlender 2000). The vineyard model was constructed using binomial logistic regression and predicts areas of possible future vineyard development based on the characteristics of areas where new vineyards were planted during 1990 to 1997. An equal number of vineyard and non-vineyard observations (100 m \times 100 m cells) were used to develop the vineyard model (in reality much less acreage in Sonoma County became vineyard than did not during 1990–1997). Thus, the probability values predicted by the vineyard model can be used as a similarity index: areas with values >0.5 have characteristics that are more similar to land that was converted to vineyard during 1990–1997, while areas with values <0.5 have characteristics that are more similar to land that remained non-vineyard during this period. We treated cells with vineyard probability scores >0.5 as suitable for future vineyard development.

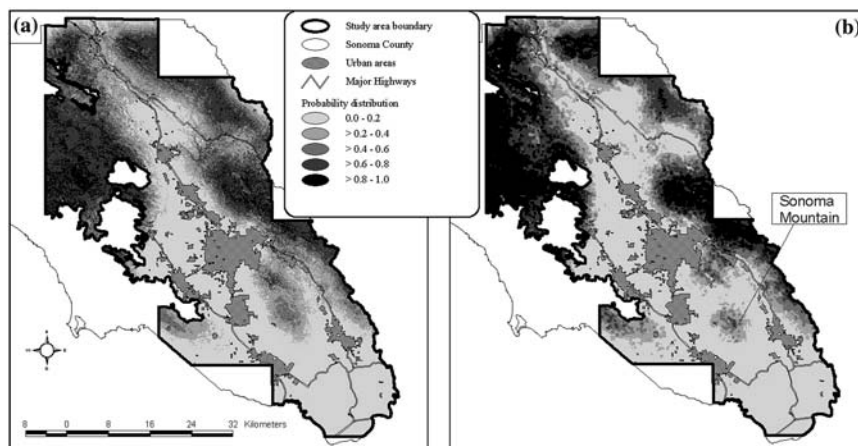


Figure 2. Estimated (a) current and (b) future probability of occurrence for native predators in Sonoma County, California.

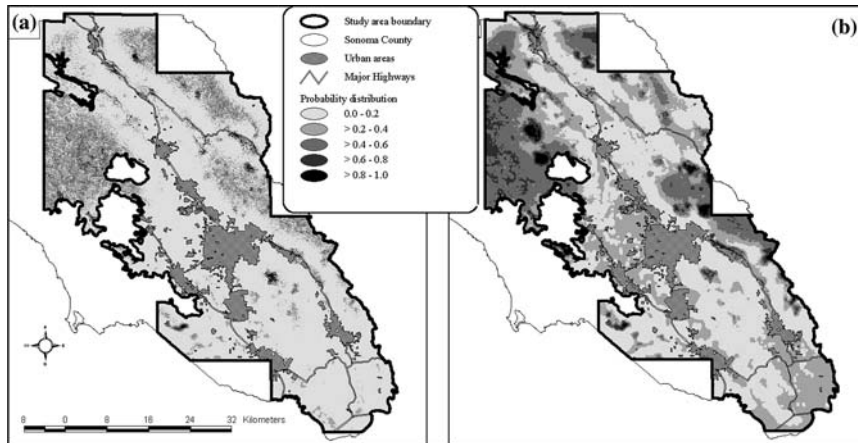


Figure 3. Estimated (a) current and (b) future probability of occurrence for non-native predators in Sonoma County, California.

Using the vineyard model, we generated probability surfaces that estimate future distributions of native and non-native mammalian predators given one vineyard expansion scenario. In the expansion scenario, all land that was considered to be suitable for vineyard development (vineyard probability >0.5) was converted to vineyard. The natural habitat/modified land GIS layer was then changed accordingly in order to generate a new layer that shows the future distribution of natural habitat and modified land with our vineyard expansion scenario. Using this new layer of future natural habitat, the landscape variables listed in Table 2 were recalculated for each cell, and the values were plugged into the logistic regression models to generate probability surfaces that show estimated future distributions of native and non-native predators (Figures 2 and 3). To view the areas of the greatest change, the probability surface for the current landscape was subtracted from the probability surface for the future landscape, both for native and non-native predators. The resulting surfaces, which show areas of likely change, are shown in Figure 4.

It should be noted that the land identified as suitable habitat for vineyard expansion (vineyard probability value >0.5) included a large amount of land that will likely never be converted to vineyard given economic and other restraints; in addition, areas that have vineyard probability values <0.5 may be converted to vineyard. We used this maximum development scenario (e.g., Swenson and Franklin 2000) because it allows for a broad estimate of natural habitat areas that are vulnerable to vineyard expansion, highlighting areas that are higher priorities for conservation where predators would be hit hardest if rampant expansion occurred. This is one illustration of how to integrate such models, and this process could be repeated for other development thresholds.

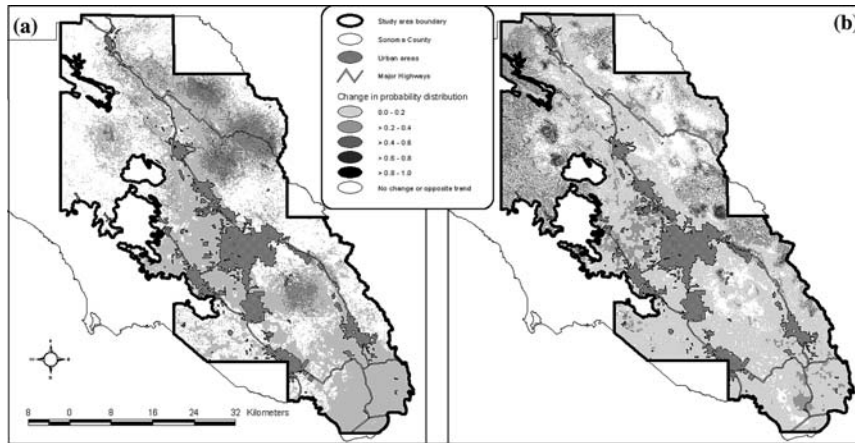


Figure 4. Subtracting the probability surface for the current landscape from the probability surfaces for the (a) native and (b) non-native species future scenarios illustrates areas where current and future probability surfaces differ the most. For native species, areas of high differences are where the probability of occurrence has decreased, and for non-natives high differences indicate increased probability of occurrence.

The choice of the threshold ultimately depends on the risk and comfort levels of those using the models for planning purposes (Wilson et al. 2005).

Results

The best-fit mixed stepwise logistic models incorporated landscape variables for both native and non-native mammalian predator models (Table 3). A higher diversity of habitats and more habitat from 500 to 4000 m around any point in the landscape increased the probability of native species occurrence, while less natural habitat and a lower diversity of habitat nearby influenced non-native species occurrence. In addition, occurrences of non-native predators were explained, in part, by the probability of native predators occurring at a given camera location (Table 3). The current and future probability surfaces for native and non-native mammalian predator occurrence illustrate how the distribution of native and non-native species may change given one scenario of vineyard development (Figures 2 and 3). The logistic regression model suggests a positive relationship of native species occurrence with non-native species occurrence, despite notable situations in large vineyard areas where native occurrence is predicted to be low and non-native occurrence is predicted to be high. (Figures 2 and 3).

Native mammalian predator models generally suggested a higher current relative probability of occurrence across the study area than non-native mammalian predators. In the future scenario, the areas of relatively high probability values became smaller and more isolated for native predators. In

Table 3. Parameter estimates for the mixed stepwise logistic models testing all variables.

Species	Term	Coefficient	S.E.	χ^2	<i>p</i>
Non-native	Intercept	-0.6820	0.8663	0.62	0.4311
	(A) Diversity of habitat types within 500 m ²	-0.3770	0.1739	4.70	0.0302
	(B) Amount of all natural habitat within 500 m ²	-0.0533	0.0112	22.59	< 0.0001
	(C) Probability of native species occurrence	8.0581	1.6253	24.58	< 0.0001
Native	Intercept	-5.5474	1.3705	16.38	< 0.0001
	D) Diversity of habitat types within 500 m ²	0.3739	0.1435	6.79	0.0092
	(E) Amount of all natural habitat within 500–4000 m	0.0011	0.0003	11.49	0.0007

*Correlation between *Y*-variables: A and B = 0.08; A and C = 0.49; B and C = 0.36; and D and E = -0.18.

contrast, the relatively small areas indicating high probability of occurrence of non-native mammalian predators became larger in and adjacent to the predicted agricultural development (Figure 4). The overall differences between the current and future probability surfaces were larger for non-natives than for native species (Figure 4).

Discussion

These models illustrate one method of using species' distribution models and land-use change models to examine the potential effects of land-use change scenarios on wildlife distributions. Such models may be useful for individuals and organizations interested in or mandated with maintaining native species across landscapes. The use of models such as these can help to forecast the impact of different human development scenarios of wildlife species. Our results demonstrate how the configuration of the landscape could influence the probability of occurrence of predators. More traditional habitat models such as those generated by California Wildlife Habitat Relationships for species rely on expert opinion and do not account for landscape configuration when estimating species occurrence, but our results corroborate an increasing number of other studies that indicate it is important to account for landscape configuration when estimating patterns of species occurrence (Bolger et al. 1997; Gascon et al. 1999; Ricketts et al. 2001).

The explanatory models suggest that vineyards, an extensive type of land use in Sonoma County (59,891 acres in 2002, Agricultural Commission 2002), appear to impact the distribution of the mammalian predators. In general, these modeled native carnivore probability distributions generate a hypothesized higher probability of occurrence across the current landscape as

compared to non-native predators. The models also suppose that native species may have lower probabilities of presence (generally $p < 0.2$) in large vineyard blocks than in isolated vineyards surrounded by habitat and in natural habitat, a contrast to the generated non-native species models.

The finding that landscape variables may impact species' distributions is important for several reasons. First, optimum niche space in the landscape, or areas with a high probability of occurrence, is where species are likely to have higher densities and be more resilient to human and environmental perturbations (Araújo and Williams 2000). Persistence of any species in a region depends on the density and proximity of populations in the region, which are likely to change as the landscape is transformed. Thus, areas with a low probability of occurrence as well as small isolated areas with high suitability are not likely to support the focal species (e.g., Beier 1993). Additionally, these analyses support a growing body of evidence that landscape characteristics beyond site-specific characteristics, may impact species' distributions (Bolger et al. 1997; Massolo and Meriggi 1998; Drapeau et al. 2000). Finally, with regards to wildlife conservation planning and management, these models illustrate the importance of looking beyond habitat loss and fragmentation toward understanding how species respond to the landscape configuration of remnant habitat and matrix.

To illustrate the utility of using species' distribution models and land-use change models, we chose one future maximum development scenario of expanding agriculture to assess the potential change of mammalian predator distribution across the landscape. This exercise indicated a reduced probability of occurrence of native carnivores across the region as well as an increase of non-native species occurrence in several locations compared to the current model prediction. Where agriculture was predicted to expand, the probability of native species occurrence decreased from $p > 0.2$ – 0.8 to $p < 0.2$. However, these decreases only occurred in a few discrete regions. In contrast, non-native mammalian predator probability of occurrence increased – from $p < 0.2$ to $p < 0.2$ – 1.0 – not only in the regions where native probabilities decreased, but also in a number of additional regions. These results suggest that non-native species probability of occurrence would increase more than the drop in native species given the same changes in land use. Land-use change models without species models would lack the ability to predict how the spatial configuration of habitat influences probability of occurrence and would not indicate the different affect of changes on native and non-native species.

The above relationships from the model analyses serve as hypotheses that should be tested with further research. We can also hypothesize, based on other ecological studies as to why such spatial patterns may occur, but further research would be needed to establish causal relationships. For example, native mammalian predators studied are not habitat specialists and utilize edge degraded habitat, so we would not expect their decline to be disproportionate to habitat loss as with more sensitive species (Bender et al. 1998). Many non-natives thrive along habitat edges and in human impacted areas (Arango-Velez and

Kattan 1997; Crooks and Soulé 1999; Hawkins et al. 1999). Because increased habitat fragmentation often initially creates more edge habitat than the amount of habitat destroyed, these non-native edge species may increase disproportionately as patches become smaller and the amount of edge habitat increases (Bender et al. 1998).

These current and future probability distribution models are useful tools for land-use managers because the probability surfaces identify areas where native wildlife are more likely to be supported today, and estimate the changes to wildlife distributions that may result due to additional habitat conversion. Forecasting where species may experience fragmentation can allow planners to pro-actively conserve key connectivity zones before development is imminent and conservation costs are high (Ahern 1995). Specifically, by identifying areas with high native species occurrence and a high probability of becoming fragmented according to forecasted development, conservation planners can prioritize the protection of vulnerable wildlife corridors. In addition, modeling non-native species expansion given different human development scenarios is important given that non-native mammalian predators often have impacts on other non-native fauna (Crooks and Soulé 1999; Hawkins et al. 1999).

The illustrated model outputs show several key areas where probability of occurrence of native species dropped from high to low and where once continuous populations of species may be relegated to small fragmented populations. For example, the models suggest a relatively high probability of occurrence of native carnivores across the Sonoma Mountain region, but the future probability surface supposes a smaller and more isolated area of high probability of occurrence surrounded by lower probability areas (Figure 2). Results of such models can illustrate where landscape connections may be lost, which could potentially result in the loss of native carnivores (Brosset et al. 1996; Machtans et al. 1996). In the case of Sonoma Mountain, those interested in wildlife conservation and corridor planning may use such models to prioritize the protection of specific sites that will provide habitat connectivity in the future.

Models such as these are tools to explore the potential impacts of human development on wildlife. In addition to using this approach with vineyard development models (e.g., Heaton and Merenlender 2000; Fairbanks et al. 2004), other types of human development scenarios, such as urban and ex-urban expansion, could be examined (e.g., Hansen et al. 2002). These models also could help direct conservation efforts toward specific regions of likely future human and wildlife conflict.

Although these models illustrate a useful tool and generate hypotheses about wildlife distributions, these models were limited by available data. Given the small available data set, we did not set any data aside to test the model. The sampling of predator occurrence was limited to one side of the valley and within two landscape features, vineyard and corridors adjacent to creeks and then extrapolated out across the oak woodland and vineyard landscape. It is possible that this limited sampling over- or under-inflates species occurrence

across the parts of the landscape not sampled. Future research is needed to test the modeled distributions of these focal species and their response to change in the landscape. Also, while covering a large geographic area, the camera locations within the each sampled creek and vineyard were close enough together to fall within a single animal's home range, making them non-independent. Defining at what scale the sampling points would be truly independent is difficult because the various landscape variables being used operate at different scales.

A thorough discussion of the uncertainties associated with the type of species occurrence models that we developed can be found in Elith et al. (2002). Many sources of error are difficult to control when taking advantage of existing digital data developed at different spatial scales in different years for calculating independent variables and using logistic regression modeling techniques. These include classification errors of data obtained such as through remote sensing (most of our data layers lack formal accuracy assessments), problems with spatial autocorrelation, and the over-simplification of the resulting statistical models; and these errors ultimately reduce the accuracy of model outcomes.

A significant source of error for the dependent variable are the possibility of high rates of false-negatives, which occur when a species is considered absent when in fact it is present. Rates of false negatives can be very high with commonly practiced survey techniques such as spot lighting (Lindenmayer et al. 2001) and other rapid methods. Remotely triggered cameras continuously sample and therefore have a low false-negative rate if used for a sufficient amount of time to detect the focal species. We calculated the average time needed to detect a species and surveyed more days than what was required to reduce the number of false-negatives and optimize our monitoring effort. More problematic for camera surveys is ensuring full coverage of the site being monitored given the camera only consistently detects wildlife within about 5m from the camera. We attempted to minimize this problem by using enough cameras to provide comprehensive coverage of sites. However, even with these precautions we may still have a small number of false-negatives in our data, especially if we consider natural variation across seasons and years (Elith et al. 2002), which only long-term studies can account for.

A useful study of the consequences of false-negative errors on the statistical estimation of habitat models based on logistic regression was done by Tyre et al. (2003) and demonstrated that the effect of a habitat variable on species occupancy is mostly underestimated if there are modest amounts of false-negatives (20–60%). Given the sensitivity of these models to false-negatives, they advocate repeated surveys to determine optimal monitoring strategies that will reduce the number of false-negatives below the level that will significantly influence model outcomes. We have done this by using remotely triggered cameras for the optimal number of days to effectively detect the focal species.

In summary, these models demonstrate a method of combining species' distribution models with land-use change models to explore the effects of land-use

change scenarios on wildlife. Such models can be used to highlight areas that wildlife biologists, land-use planners, and communities might want to consider for conservation activities, such as areas that enhance or maintain connectivity. They also provide a tool to explore the importance of various landscape variables as well as interspecific interactions on species' distributions, both of which could influence species' persistence in fragmented landscapes.

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