

Pumas' fear of humans precipitates changes in plant architecture

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Abstract. Fear of predation can elicit strong behavioral responses from prey, with impacts that cascade through food chains. While this indirect effect of natural predators on ecosystems is becoming better understood, far less is known about how humans—the world's most ubiquitous super-predator—influence subsequent trophic levels through changes in carnivore habitat use and behavior. Here, we combined puma GPS tracking data with field experiments to understand the extent to which anthropogenic development has cascading impacts from pumas to plants. We examined spatial patterns in puma feeding sites and found that pumas preferentially kill deer away (>340 m) from human development. This aversion appears to create refugia for deer, as deer more than doubled their relative activity near (<70 m) human development. In addition, deer more than quadrupled their consumption of woody vegetation at low-risk sites close to humans relative to comparable high-risk sites far from humans and consumed a greater percent of the forage available in sites near humans than in comparable sites farther away. Increased browsing by deer in near human, or low-risk, sites induced woody plants to become bushier (by removing apical dominance) than those away from humans, or high-risk sites. The cascading interactions from pumas avoiding people to changes in plant architecture appear to have increased available food to deer (i.e., bushier plants have more available branch ends providing potential bites of food than less bushy individuals) and may have other, as yet undocumented, ecological effects.

Key words: anthropogenic development; herbivory; plant architecture; predator avoidance; predator–prey dynamics; trophic cascades.

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INTRODUCTION

Differences in plant morphology can have important effects on ecological communities, affecting ovipositing behavior and prey refugia (Lawton 1983), species composition and diversity (Lawton 1983, Crutsinger et al. 2010), soil moisture availability (Classen et al. 2007), and erosion (Bochet et al. 2006). Herbivores

influence these dynamics by precipitating significant changes in plant abundance and architecture through selective browsing on palatable plants (Ford et al. 2014), repeated browsing (De Jager and Pastor 2010), and preferentially foraging in certain habitats (Donadio and Buskirk 2016). There is also a large body of literature documenting carnivore impacts on plant communities via indirect effects (Schmitz et al.

2000, 2004, Terborgh and Estes 2010, Ford and Goheen 2015, Ripple et al. 2016), but few studies have addressed the role of trophic cascades in shaping plant architecture.

Trophic cascades have been found across many habitat types and species communities (Schmitz et al. 2000, 2004, Terborgh and Estes 2010, Ford and Goheen 2015, Ripple et al. 2016), and anthropogenic habitat modification has been documented globally as well. Recent research has shed new light on how human activities extend beyond the urban–wildland interface, impacting carnivore space use (Berger 2007, Wilmers et al. 2013, Suraci et al. 2019), influencing community dynamics (Hebblewhite et al. 2005, Wang et al. 2015, Suraci et al. 2019), contributing to species decline (Gibbons et al. 2000), and altering ecosystem function (McKinney 2002), but few have addressed the indirect effects that humans have on plant morphology.

In a tri-trophic cascade, predators limit prey density and/or change prey behavior, indirectly benefiting local primary producers (Paine 1969, Estes and Palmisano 1974, Power 1990, Schmitz et al. 2000, 2004, Hebblewhite et al. 2005, Ford and Goheen 2015, Donadio and Buskirk 2016). Human activities can add an additional super-predator-like trophic level, strongly mediating trophic interactions by directly or indirectly influencing carnivore abundance or behavior (Hebblewhite et al. 2005, Ripple and Beschta 2006, 2008, Waser et al. 2014, Darimont et al. 2015, Clinchy et al. 2016, Smith et al. 2017, Suraci et al. 2019). Much like gaining an additional trophic level to the system, humans have both consumptive (hunting, lethal removal, poisoning, roadkill, etc.) and non-consumptive effects on predators (disrupting behaviors, aversive stimuli, impeding movement, etc.), thereby lowering predator density and/or altering their habitat use (Hebblewhite et al. 2005, Ordiz et al. 2011, Wilmers et al. 2013, Patten and Berger 2018).

Prey respond to shifts in predation risk, behaviorally or numerically, changing where and to what degree they forage (Lima and Dill 1990, Lima 1998, Schmitz et al. 2004, Ripple et al. 2016). Potentially leveraging these dynamics to their advantage, prey may use human activities as a shield against predation (Martin and Szuter 1999, Ripple and Beschta 2006, 2008, Berger 2007, Muhly et al. 2011, Steyaert et al. 2016). Heavy

grazing or browsing in preferred safe prey habitat can significantly impact plant abundance, shifting species composition toward less palatable vegetation (Augustine and McNaughton 1998, Ford et al. 2014). In this way, a super-predator can have impacts extending throughout the community, ultimately restructuring plant morphology (Beschta and Ripple 2012, Mathisen et al. 2017), with potential ecosystem feedbacks.

Here, we studied the dynamics of pumas (*Puma concolor*), black-tailed deer (*Odocoileus hemionus columbianus*), and woody plant species in the context of human development. We addressed three interlocking hypotheses to elucidate the nature of interactions among these species: (1) human activity drives puma feeding site selection, (2) predation risk influences relative deer activity, increasing the relative rate of deer browsing in low predation risk areas, and (3) increased deer activity in low-risk areas will influence woody plant architecture (Fig. 1). We studied these dynamics in the Santa Cruz Mountains, California. Pumas, deer, and woody plants are each widely distributed across the Americas, making the results of this study highly applicable to a broad geographic area. In addition, as the human population grows, it further increases the likelihood and spatial extent of these interactions.

MATERIALS AND METHODS

Study area

We conducted our study in the Santa Cruz Mountains of California (Fig. 2), where the climate is Mediterranean with hot, dry summers, and cool, wet winters. The 1600-km² study area ranges from sea level to 1155 m in elevation, with two distinct climactic zones. The coastal west side is cooler and wetter, with average high and low temperatures of 20° and 7.5°C, respectively, and 77 cm annual rainfall. Vegetation is dominated by mixed evergreen forest, with redwood (*Sequoia sempervirens*), tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), and Douglas fir (*Pseudotsuga menziesii*), interspersed with chaparral and grassland. On the inland east side, average high and low temperatures are 33° and 1°C, respectively, with 46 cm annual rainfall. Vegetation is dominated by chaparral on south- and west-facing slopes, with mixed oak (*Quercus*

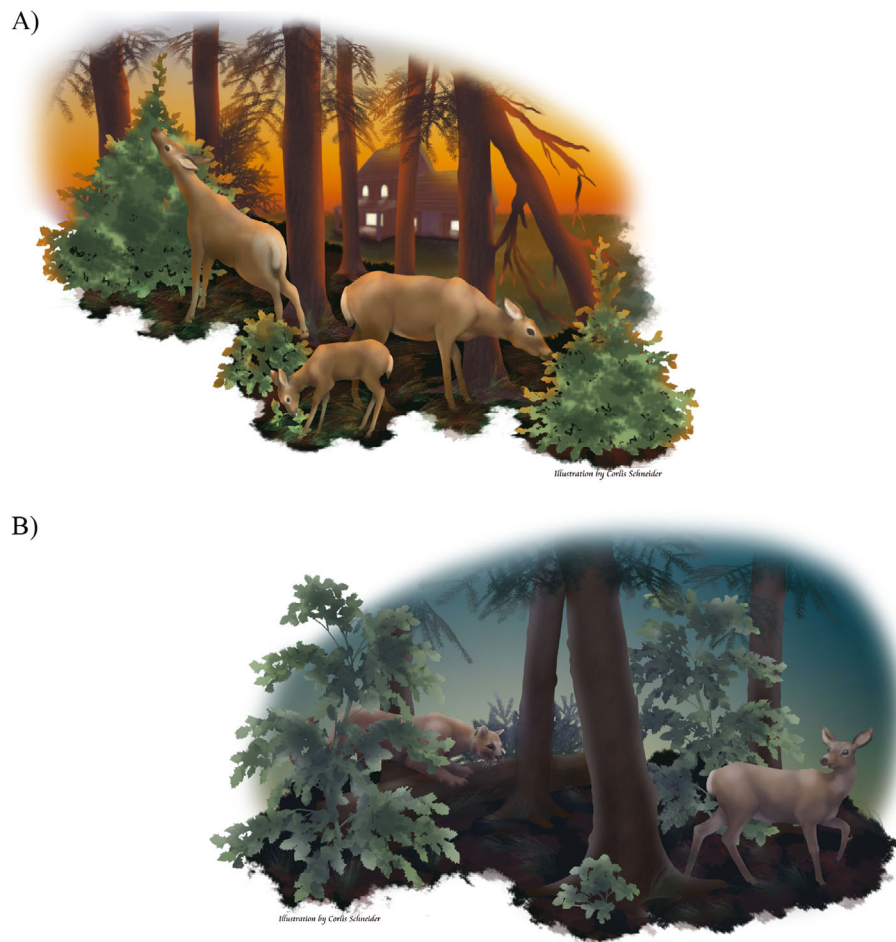


Fig. 1. Pumas avoid hunting near human development, making habitat close to humans relatively safer for deer. In response, deer increase their relative use of areas adjacent to development by increasing browsing pressure, which removes new growth and promotes lateral bud development. The heavier browse pressure increases structural complexity in woody plants near human development (A). Altogether, the human-induced cascade makes bushes growing near human development bushier (A) than bushes in areas farther from humans, where pumas are more active, deer do not browse as heavily, and woody plants grow fewer branch ends (B).

spp.), bay laurel (*Umbellularia californica*), and tanoak on north-facing slopes. Vegetation communities are highly diverse and heterogeneous, and composition depends upon the distance to the ocean, elevation, slope, and aspect. In the dry season, herbaceous plants die back leaving mostly woody species remaining. The study area also encompasses a range of human development and protected lands, creating a mosaic of land use. There are large blocks of private or government-managed preserved habitat, interspersed with human-dominated areas ranging from rural to urban development with housing

density of 0–40 units per acre, as well as trails, fire roads, residential roads, and highways. Though pumas in our study area are no longer hunted, interactions with humans (e.g., animals shot for livestock predation, automobile collisions, poisoning, etc.) remain the leading source of puma mortality (Wilmer, unpublished data).

Animal captures and monitoring

We captured 25 pumas (15 females and 10 males) from 2008 to 2014 with cage traps, leg hold snares, or trailing hounds as described in Wilmer et al. (2013). Individuals were tran-

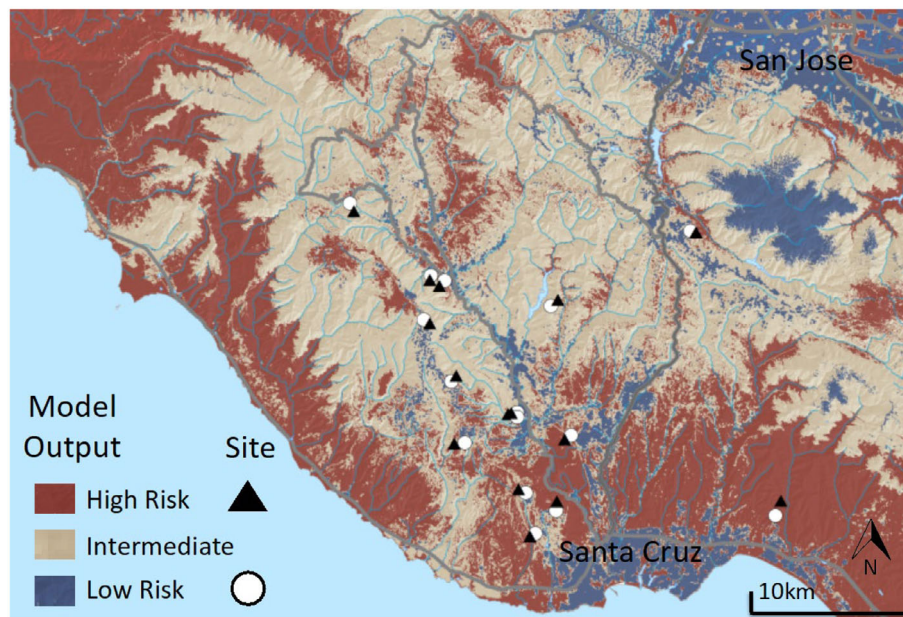


Fig. 2. Predation risk map in which model output depicts blue areas as those with low predation risk and red as areas with high predation risk. Sites consisted of paired plots, one plot in high-risk habitat (black triangle) and one in low-risk habitat (white circles). All sites were placed in closed-canopy forest, and we controlled for differences in slope, aspect, canopy closure, and forest composition within pairs.

quilized using Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa, USA) and outfitted with a GPS/VHF tracking collar (Vectronics Aerospace GPS PLUS model, Mesa, Arizona, USA). Collars were programmed to acquire a GPS fix every 4 h. Data were remotely downloaded monthly via UHF or transmitted via cell phone towers every 1–3 d depending on collar program configuration and local cell phone coverage. Puma capturing, handling, and monitoring protocols were approved by the Animal Care and Use Committee at the University of California, Santa Cruz (protocol Wilmc1101), and by the California Department of Fish and Wildlife.

Statistical analyses

Human influence on puma hunting behavior.—We analyzed the spatial relationship between puma feeding sites and human development to model how habitat variables influence feeding site selection and, by extension, deer predation risk. As ambush predators, pumas rely on stealth and surprise to rush deer with little or no pursuit. These feeding site locations represent the result of a predator–prey game in which pumas hunt

deer and deer attempt to avoid predation. Though deer may avoid habitat types where the risk of predation would be greatest, as that could mean certain death, kill site locations provide a reasonable proxy for where predation risk is functionally highest, or habitat utilized by deer where the threat of predation is most considerable. We used a resource selection function (RSF) to model relative puma preferences for habitat features (Manly et al. 2002). Resource selection functions allow us to model the proportional probability of resource use by comparing habitat covariates in used sites relative to its availability within an individual puma's home range (Boyce et al. 2002).

We identified used points (puma feeding sites) using puma GPS collar data. We adapted an algorithm developed by Knopff et al. (2009) to identify spatially aggregated GPS locations as potential puma feeding sites for large prey items. Previous research has determined that GPS data may be used to accurately predict the locations of large prey, defined as mammals >8 kg (Knopff et al. 2009), as such we chose to restrict our definition of a feeding site to places where pumas

killed deer. We verified potential feeding site locations with field site visits and collected data on whether prey remains were found. These data were fed into a logistic regression model to estimate the probability of whether each GPS cluster was a feeding site. Clusters in which prey remains were located and likely feeding sites identified by the algorithm were considered used points for analyses (for full feeding site identification, cluster investigation methods, and predictive feeding site probability algorithm, see Wilmers et al. 2013). Pumas with only one verified feeding site were eliminated from the analysis, as were juveniles and kittens. Each of the i model variables, x , was normalized as follows,

$$x_i^{\text{norm}} = (x_i - x^{\text{mean}}) / \text{SD}$$

In our study area, pumas kill a deer once a week on average (Smith et al. 2015), a time period sufficiently large for a puma to traverse its entire home range between kills. As such, we drew available comparison locations at random from within each puma's home range. Specifically, we created a 95% minimum convex polygon (MCP) from each puma's GPS collar data and generated random points from each MCP at a rate of 5 available random points for each used feeding site location (e.g., Johnson and Gillingham 2005).

For each used and available point, we quantified habitat data by extracting underlying GIS layer information in ArcGIS (v.10.1; ESRI 2011). We created a distance to feature raster layer for each anthropogenic feature (roads and structures) and landscape features (rivers and lakes); each raster layer had a resolution of 30 m. We categorized roads into two groups depending on their speed limits: arterial roads with speed limits of 35 mph or greater, and neighborhood or fire roads with speed limits below 35 mph. We created a housing density map by combining county-level spatial housing data with digital aerial photographs of the study area; we superimposed the two layers and hand-selected visible structures absent from the housing data. We then created a housing density raster layer by applying a kernel with a scale parameter to the location of each structure and summing the resulting densities. In order to evaluate how best to model puma behavioral responses to housing density, we used a variety of scaling parameter values

and chose the most appropriate value as determined by ΔAIC .

We used four scales of vegetation cover (US Geological Survey, Gap Analysis Program May 2011, National Land Cover, Version 2) to determine which resolution was most appropriate for our analysis. Scales ranged from a resolution of 26 vegetation community types, to a binary vegetation layer in which 0 was open habitat and 1 was habitat in which the year-round dominant vegetation is sufficient cover to conceal a stalking puma. We defined vegetation sufficient to conceal a puma as shrubby plants or trees growing to puma shoulder height (52 cm) or above. In our study system, woody vegetation communities, such as chaparral, and coastal scrub, are typically above puma stalking height, whereas herbaceous communities, such as annual grassland, are typically shorter-statured plants below this height.

Top trophic level: puma predation risk model.—We created a resource selection function (RSF) to model landscape predation risk (Manly et al. 2002). Feeding site locations served as the used points, and we modeled the relative probability of resource use with a generalized linear mixed-effects model with a binomial link (lmer package in R version 2.15.0; Johnson et al. 2006). Used/available was our binomial dependent variable, and habitat variables were fixed effects. In order to account for variation in individual preferences, we included individual puma identity as a random effect. We selected the best model by comparing ΔAIC values for full and reduced models.

We included anthropogenic feature, vegetation, and topographic feature covariates as predictor variables in our model. In order to determine which housing density kernel was appropriate for analysis, we varied the housing density scaling parameter from 10 to 200 m in 10 m increments and 200–600 m in 100 m increments and compared competing models using ΔAIC . We used the same incremental process to determine the appropriate vegetation classification scheme. We compared ΔAIC for each full model, as well as each full model plus one vegetation classification level in order to determine which resolution was most appropriate.

Next, we used the predation risk model to map high and low probability puma feeding

sites, or high and low predation risk areas. We considered a relative probability of 25% or below to be low-risk and a relative risk of 75% or above to be high-risk. Human development was the single strongest factor influencing predation risk for deer (Table 1). As such, we held other variables constant and varied housing density to determine high-risk and low-risk sites. We measured the average distance between high- and low-risk areas to the nearest human development edge to determine high- and low-risk plot configuration. When selecting potential plots, we checked sites against the model output to ensure that each was accurately assigned as high- or low-risk.

Middle trophic level: puma influence on deer space use and foraging behavior.—We conducted a randomized block design study to test the impact of housing density and predation risk on deer habitat use. We established 15 pairs (1 low-risk and 1 high-risk) of plots; each pair is referred to here as a site. Low-risk plots were located between 70 and 100 m from the nearest human development, while high-risk plots were 340–400 m away from development. This arrangement provided one experimental factor (risk) with 15 replicates for each of the two levels. We selected plots within closed-canopy forest and matched vegetation type within pairs (e.g., paired redwood low-risk plots with redwood high-risk plots, paired mixed deciduous stands, etc.) to minimize site-level habitat differences. All plots were located within forested areas, and edge habitat was defined as boundaries between changes in habitat types. We then verified our selection by comparing the plots with statistical tests. We used paired *t*-tests to compare slope, aspect, elevation, distance to edge habitat, and

the distance to the nearest river as determined from GIS layers (Bates et al. 2015). We took digital hemispherical canopy photographs using a fish-eye lens facing north, mounted 1 m high to calculate percent canopy closure using Gap Light Analyzer v.2 (Frazer et al. 1999), and used a paired *t*-test to evaluate differences in canopy cover. We deployed a motion-detecting camera (Bushnell Trophy Cam HD; Bushnell, Overland Park, Kansas, USA) on a game trail in each plot from the winter of 2012 through winter of 2013 to collect data on relative deer abundance. Cameras were mounted 0.5–1 m high, and programmed to take three photographs when triggered, with a one-minute lag between bursts. Unmarked deer cannot be accurately uniquely identified, so we calculated a relative deer activity index for each plot (deer photographs/camera days at each plot). We compared deer activity in high-risk vs. low-risk plots using a paired *t*-test. Since deer activity data were non-normal, we tested a series of transformations and $x^{0.2}$ best normalized the data.

We measured foliar nitrogen to evaluate potential anthropogenic changes in nitrogen availability and potential corresponding changes in browsing rates in high- vs. low-risk sites. We also measured leaf tissue carbon to nitrogen ratio (C:N) to evaluate plant tissue palatability and nutritional content in high- and low-risk plots; lower C:N ratios indicate higher nutrition content and greater palatability (Bryant et al. 1983). We additionally compared foliar C:N in browsed vs. unbrowsed plants to determine whether tissue quality shifted in response to herbivory.

During the last week of April and the first week of May 2013, we collected tanoak leaf samples from all plots. Tanoak was selected for analysis because it was the most heavily utilized browse species and found in all sites. Ten leaf samples were collected from each plot, five samples from unbrowsed plants and five from browsed plants. Plants were selected randomly along the browse survey transect, and samples were collected from branches originating from a height of 20–50 cm. In order to control for leaf developmental stage, leaves from the current year's growth were collected. Leaves were stored in coin envelopes and dried at 65°C for 48 h.

We sampled 0.10 g from each leaf and pooled samples by plot and browse status. The pooled

Table 1. Best fit RSF for puma feeding site selection.

Habitat covariate	Coefficient	SE	<i>P</i>
Distance to community scrape	0.066	0.027	>0.01*
Distance to road	−0.165	0.031	>0.01*
Slope	0.103	0.027	>0.01*
Elevation	−0.100	0.032	>0.01*
Distance to river	−0.087	0.027	>0.01*
Sex	−0.026	0.073	0.72
Housing density	−0.342	0.051	>0.01*
Vegetation cover	−0.040	0.052	0.44

Notes: Sample size for feeding sites was 1980, and 9,900 for random points. Asterisks denote significant *P* values.

sample was homogenized in a ball-mill grinder for seven minutes to create a fine powder. Three milligrams of each pooled sample were loaded into tin capsules and used to measure leaf nitrogen and carbon concentrations with a Dumas-style combustion analyzer (EA 1108 Carlo Erba). All analyses were conducted at the University of California, Santa Cruz Stable Isotope Laboratory. We used a mixed-effects model with risk level, browse status, and their interaction as fixed effects and site as a random effect to compare leaf N content and C:N ratios from high- vs. low-risk plots and from browsed vs. unbrowsed plants.

We used program R (v.3.0.0; R Core Team 2013) for our statistical analyses. Before performing each statistical analysis, we tested each continuous variable dataset for normality with Shapiro-Wilk's normality test and tested for homoscedasticity of variance with Levene's test. Non-normal data were transformed as noted below.

Lower trophic level: deer influence on plants.—In the fall of 2013, we surveyed woody plant species and browse pressure in each site. In the study area's Mediterranean climate, fall rains stimulate herbaceous plant growth, providing a relatively more palatable food source over woody plants. We conducted browse surveys in the fall, just after deer shift from relying on woody plant species to consuming herbaceous plants (Gogan and Barrett 1995). In addition to being a critical seasonal food source, woody species persist year-round and hold the marks of previous and current herbivory. This standing record serves as an important metric for assessing deer use, which can be used as a proxy for their perception of predation risk across space and time (Beschta and Ripple 2013).

We used a line-intersect method, as described by Cummings and Smith (2000) to measure woody plant species composition, abundance, browse availability (bites available), and browse use (bites taken and percent of bites consumed). We measured woody vegetation grown during the current season with a height below 2 m that fell within 1 m of a 25 m transect, as 2 m is the maximum height deer can reach while feeding (Gill 1992). We measured growth from the current year; it is the most palatable and most likely to be selected. The following data were

collected: species, number of bites available, number of bites taken, and a binary classification of whether there were signs of browse from previous years (0 = none, 1 = one or more browsed branches). Bites were defined as a group of leaves likely to be taken as a single bite based on size and position on the branch, or as bitten stem ends/groups of bitten stem ends of similar size and orientation. Deer herbivory can be distinguished from rodent or other forms of herbivory based on tooth marks left behind (Swift and Gross 2014). Each branch end of every woody plant occurring along the transect was examined to determine bites available, bites taken, and bites remaining.

We compared wood plant species composition in low- vs. high-risk sites using nonmetric multidimensional scaling of Bray-Curtis similarity estimates. We visually assessed potential spatial grouping of points in the similarity plots (Legendre and Legendre 1998). We also compared browsable plant density in low-risk and high-risk sites using a paired *t*-test.

We compared herbivory pressure in low- vs. high-risk plots in several ways. First, we calculated percent consumption by dividing the number of bites taken by the number of bites available (taken plus remaining) for each plot. We also calculated a relative index of browse pressure per deer unit by dividing the total number of bites taken within a site by the number of deer photographed per day. We use paired *t*-tests to compare browse intensity. We normalized the percent of plants with evidence of previous browsing with a square root transformation and then compared high- and low-risk plots with a paired *t*-test.

RESULTS

Puma feeding site selection

We visited 777 GPS clusters from 25 pumas, and located prey remains at 265. Using these data to train our kill prediction model (Wilmers et al. 2013), we were able to identify an additional 1,715 probable feeding sites, for a total of 1,980 used points. Our analysis revealed that feeding site selection was best fit by an RSF model with a housing density scale parameter of 75 m and a binary vegetation classification scheme. The remaining habitat covariates

retained in the reduced model were the distance to the nearest community scrape, road with a speed greater than 35 mph, and river; slope; elevation; housing density; sex; and vegetation cover (Table 1). The single strongest covariate influencing puma feeding site selection was the proximity to human development. The average distance between human development and predicted low-risk areas (a relative risk of 25% or lower) was 70 m, and the average distance between human development and high-risk areas (a relative risk of 75% or greater) was 340 m (Fig. 2).

Deer browse and relative activity

We found no significant differences in slope, aspect, elevation, canopy cover, or distance to forest edge between high- and low-risk plots (Table 2). We also found no significant difference between high- and low-risk sites for tanoak leaf percent nitrogen (low-risk = 1.24 ± 0.07 , high-risk = 1.26 ± 0.10 [mean \pm SE]), leaf C:N ratios (low-risk = 41.04 ± 2.04 , high-risk = 41.59 ± 2.47), and no significant difference in C:N ratios between browsed (41.61 ± 1.61) and unbrowsed (40.27 ± 1.76) plants (Table 3).

We recorded a total of 52,260 camera trap photographs collected from 30 trapping stations, each deployed for an average of 400 d (± 17). There were nearly three times as many deer visits per camera day in low-risk plots (2.94 ± 1.00) than in high-risk plots (1.13 ± 0.30 ; Fig. 3).

Table 2. Physical properties comparisons made between high- and low-risk plots.

Physical property	Low-risk		High-risk		t	P
	Mean	SE	Mean	SE		
Slope	4.69	0.88	5.19	0.72	0.61	0.55
Elevation	320.23	48.11	336.75	45.05	1.37	0.19
Distance to habitat edge	31.07	5.76	73.13	24.00	1.69	0.11
Aspect, North	-0.10	0.18	-0.12	0.13	0.11	0.91
Aspect, East	0.11	0.19	0.05	0.23	0.30	0.77
Distance to river	206.40	45.52	197.28	46.09	0.19	0.85
Canopy closure	15.98	0.72	15.29	1.08	0.53	0.60

Notes: We compared plot characteristics using a paired t-test with the site as the pair. None of the habitat variables we measured differed significantly between high and low-risk plots. (The df value for each comparison was 13.)

Table 3. Mixed effects models addressing plant tissue percent nitrogen and in C:N in high- and low-risk sites.

Fixed effects	Coefficient	SE	t	P
Plant tissue percent nitrogen				
Risk level	-0.046	0.089	-0.37	0.72
Browsed	-0.123	0.069	-1.78	0.08
Browsed \times risk level	0.138	0.098	1.34	0.18
C:N				
Risk level	2.508	3.462	0.72	0.47
Browsed	3.253	1.846	1.76	0.08
Browsed \times risk level	-3.923	2.610	-1.50	0.13

Notes: In the plant tissue percent nitrogen model, fixed effects were risk level, whether or not the sample was taken from a browsed or unbrowsed plant, and the interaction between, and site was a random effect. None of the variables in either model was significant.

Plants and browse pressure

There was no spatial segregation within the Bray-Curtis similarity plots, indicating that high- and low-risk plots within sites had indistinguishable species composition. We also found no significant difference in the density of individual woody plants within browse height in low-risk ($0.48 \text{ plants/m}^2 \pm 0.06$) vs. high-risk ($0.48 \text{ plants/m}^2 \pm 0.07$) plots (Table 4). However, there were 26% more bites available per plant in low-risk plots (7.08 ± 0.43) than in high-risk plots (5.60 ± 0.33 ; Table 4, Fig. 3). Furthermore, in low-risk plots, deer utilized available forage at a rate 4.5 times higher than in high-risk plots (low-risk = $35.82\% \pm 1.98$, high-risk = $7.94\% \pm 1.07$; Table 4, Fig. 3). There was no significant difference between high- and low-risk sites with respect to total bites taken per deer unit (low risk = 6.90 ± 0.43 , high risk = 5.79 ± 0.35 ; Table 4). In addition, the percent of plants showing evidence of browse from previous years was higher in low-risk plots ($94.29\% \pm 1.26$) than it was in high-risk plots ($87.79\% \pm 3.46$) with a large effect size ($\phi = 0.6$; Table 4).

DISCUSSION

Our data are consistent with a human-initiated trophic cascade in which human activities elicit bushier growth in woody plants adjacent to human development. In high-risk plots farther from human disturbance, deer visitation rates

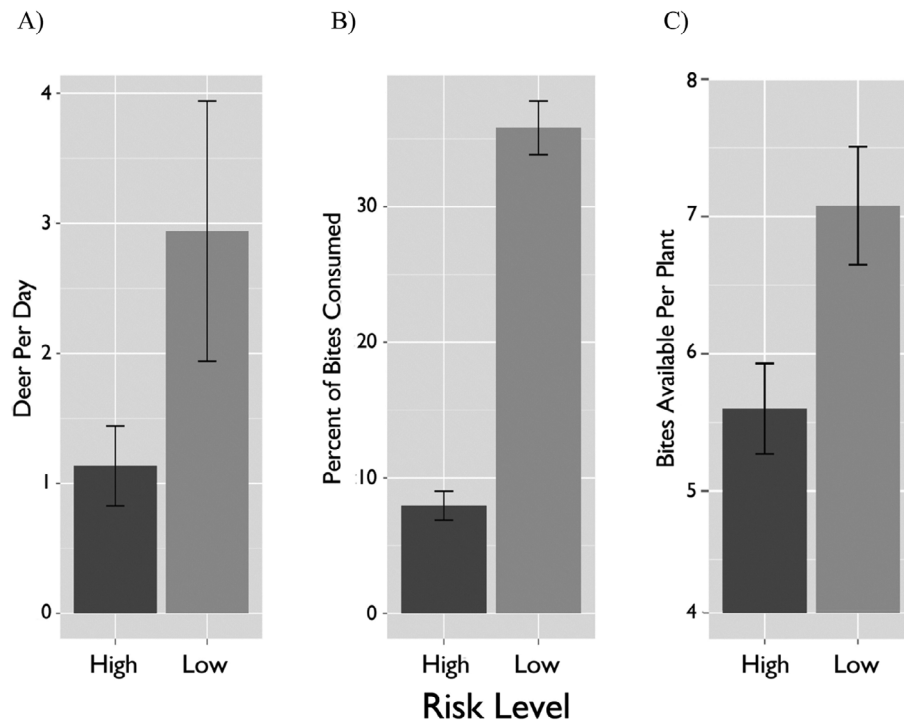


Fig. 3. Comparisons of the number of deer photographed per day (A), the percent of available bites consumed by deer (B), and the bites available per plant (C) in high- vs. low-risk plots. Bars represent mean values and error bars represent standard error around the mean. All comparisons were significant in paired *t*-tests ($P < 0.05$).

Table 4. Comparisons made between pairs of high-risk plots far from human development and low-risk plots near human development.

Comparison	Low-risk		High-risk		t	P
	Mean	SE	Mean	SE		
Browsable plant density	0.48	0.06	0.48	0.07	0.27	0.79
Bites available per plant	7.07	0.43	5.60	0.33	2.18	0.03*
Previous browse	94.29	1.26	87.79	3.46	2.38	0.03*
Percent browse utilized	35.82	1.98	7.94	1.07	4.74	<0.01*
Deer visit per day	2.94	1.00	1.13	0.30	2.19	0.04*
Bites taken per deer unit	6.90	0.43	5.79	0.35	0.89	0.39

Notes: All analyses were paired *t*-tests with $df = 13$. Asterisks denote significant *P* values.

and overall plant consumption are lower, suggesting alternating relationships of inhibition and release (Fig. 1A). In low-risk plots close to human structures, we see non-consumptive human impacts on puma feeding site selection,

with corresponding alternating influences on deer, and plants (Fig. 1B). Woody plants below a height of 2 m sustained lower browse pressure in high-risk areas and were more heavily browsed in human-dominated areas. The end result is that woody plants growing near human development grew bushier than their counterparts in habitats identical in all aspects we examined, other than predation risk.

This bushier growth pattern could create a potentially advantageous feedback for deer: By promoting dormant bud development, deer may create more abundant branch ends with higher palatability (DuToit et al. 1990), effectively pruning plants to create more abundant, higher quality forage in preferred low-risk habitat (De Jager and Pastor 2010; Fig. 1). Whether this results in a positive feedback for deer in low-risk sites in the long run will depend on how high browsing rates affect forage quality; plant structural and defensive responses to herbivory result in negative impacts on herbivores in many systems (Burghardt and Schmitz 2015). Although we saw no

differences in leaf tissue N or leaf C:N ratios for the most abundant browseable woody species in our system, additional examination of plant responses to herbivory is needed to elucidate the finer mechanisms at play here.

The changes in plant architecture we detected were likely brought about by herbivore responses to predation pressure. Two common anti-predator strategies include modifying habitat selection and changing foraging behavior (Lima and Dill 1990, Lima 1998). Other studies have documented prey capitalizing on human presence as a shield against predation by utilizing habitats adjacent to human activity (Martin and Szuter 1999, Hebblewhite et al. 2005, Berger 2007). For example, Hebblewhite et al. (2005) found that wolves in Banff National Park avoided areas with greater human activity, and as a result, elk spent more time near human structures. Similarly, pumas in our study area avoided areas occupied by humans. Our study indicates that deer respond by increasing use of plots closer to human structures relative to plots farther from humans and consumed a greater percentage of the available forage in low-risk areas. We attempted to test for changes in foraging behavior specifically by measuring deer anti-predator behavior in high- and low-risk sites; however, our experiment failed. We set out a standardized feed paired with a video camera trap in each site to compare how predation risk influenced deer vigilance rates. Unfortunately, the majority of the bait stations were urinated on by foxes, rendering them unattractive to deer. We also tried establishing feed stations off the ground to avoid this issue, but deer showed no interest in the high-quality human-provided food and proceeded to forage on native vegetation instead.

In order to ensure that the relationships we describe were derived from human-induced changes in predation risk, we explored potential alternative explanations for the observed increases in deer activity near human development (Augustine and Naughton 1998). Deer are an edge-adapted species and could have been selecting for preferred edge habitat with a more well-developed understory, rather than protection from predation. We measured distance of the plot to the closest habitat edge, canopy closure, and the number of plants within browse

height within each plot and found no significant difference between low-risk and high-risk plots in any of these metrics. Furthermore, although the number of bites available per plant was 26% higher in low-risk sites, and the stem densities of plants within browse height were equal between high- and low-risk sites, deer percent consumption of available bites was 4.5 times greater in low-risk sites. This mismatch between forage availability and percent consumption suggests that greater deer use of low-risk sites is not driven by forage availability alone.

A second alternative explanation to higher browse pressure in plots close to human development is that deer were responding to increased anthropogenic resources, such as irrigated landscapes, gardens, or other human-derived subsidies in adjacent developed areas (Fenn et al. 2003). If this were the case, we would expect to see higher relative deer activity in low-risk sites, and lower browse rates since they would be consuming the human-associated resources that attracted them to the site. Consistent with either a nutrient subsidy explanation or predator shield explanation, we did find that the number of deer visits per day was over twice as high in low-risk sites vs. high-risk sites (Table 4). Deer were not individually identifiable, so we were unable to determine whether the difference between high- and low-risk sites were from increased activity of resident deer, or increased numbers of deer passing through on their way to a human-provided attractant. To differentiate between the two explanations, we compared the relationship between risk level and the number of bites taken per deer unit, as lower browse rates would indicate use of other local resources. We found no significant difference between bites taken per deer in low-risk compared with high-risk sites, suggesting that deer fed at the same rate in low-risk sites as they would feed elsewhere, but the increase in deer activity in those sites resulted in heavier browse pressure in safe areas. Further, deer failed to consume high-quality forage from our proffered feeding plots, regardless of habitat risk level. Deer consuming unintentionally supplied human resources may be an issue in some contexts (Conover et al. 2018), but it does not appear to be as commonplace in our study area.

A third alternative explanation is that deer were attracted to plots closer to human-

dominated areas by differences in resource availability. Fertilizer and pollution from human-altered landscapes can increase plant growth rates (Fenn et al. 2003) or enhance tissue chemical composition (Vallano and Sparks 2008), by extension, increasing foraging reward in plots near development. A twist on this alternative explanation is that the additional browse pressure could induce plant tissue defenses, reducing forage nutritional availability, thereby increasing the amount of forage required to maintain equivalent nutritional requirements. In either case, we would expect to see differences in foliar chemistry. However, when we measured leaf nitrogen and C:N ratios, we found no significant differences between high- and low-risk plots, nor did we find any significant difference between browsed and unbrowsed plants (Table 4). It is possible that different chemistry could result in the same C:N; future studies could examine plant defensive chemistry in high- vs. low-risk plots. In total, our exploration of alternative hypotheses leads us to the conclusion that increased browse pressure in low-risk plots reflects increased protection against predators rather than differences in proximity to preferred edge habitat, woody plant availability, plant palatability, or the nutritional content of plant tissues.

Extending these results beyond our local study area, these trophodynamics are likely playing out over a large spatial extent. Pumas can be found across the Americas, from the southern tip of South America to the sub-Arctic. Cervids are even more widely distributed, as are the woody plants they consume. Low-density exurban development is projected to increase by over 75% in the next 25 yr (Alig et al. 2004), and so will the urban-wildland interface where anthropogenic activities abut wild habitats. The dynamics described here are likely to accompany human development, altering trophic relationships and species interactions across a broad area (Hebblewhite et al. 2005, Ford et al. 2014).

Our results support the findings from Wilmers et al. (2013) that pumas select feeding sites that avoid human development. We then extend these results, demonstrating how puma-human dynamics influence lower trophic levels. Human activities can lead to many indirect and unintended consequences. Though the impacts may be subtle at first, compounding these influences

over space and time could cause substantial and difficult to remedy ecosystem-level shifts. There are rich literatures about the effects of human development on surrounding ecosystems, as well as on trophic cascades. However, this study contributes to a new and growing field tracing human-initiated trophic cascades through ecosystems and linking them to changes in plant architecture. Further research would shed light on the influence altering plant structure has on surrounding ecosystems, how observed differences contribute to changes in individual plant life history, as well as local bird, invertebrate, or non-woody plant species composition.

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