

**More Than Charismatic:
The Role of Pumas in Driving Composition of Bay Area Vertebrate Communities**

Ben Greenberg Pridonoff

ABSTRACT

Human society depends on intact and healthy ecosystems for ecosystem services, sustenance, and recreation. However, a potentially key facet of ecosystem conservation is omitted from many management strategies. Large apex predators, such as *Puma concolor* (also known as the puma, mountain lion, or cougar), are not considered for their ecological importance. Studies suggest that these dangerous predators effectively regulate the composition of their animal and even plant communities through predation, competition, and fear. Thus, in the effort to preserve community compositions that support ecosystem health and stability, managers should consider the influence of predators, despite a paradigm of neglecting their often-immense impacts. This study sought to investigate an example of community composition differences by surveying two sites with significantly different puma populations. By studying key aspects of the community, such as coyote occupancy, I found compelling evidence to suggest a trophic cascade has occurred in the site with a collapsed puma population. Where less pumas were present, I observed greater mesopredator occupancy (probability estimate = 0.814, over 0.704) and lower small mammal diversity (-0.46, compared to 0.44, $p < 0.05$), indicating pumas act as both a regulator of damaging opportunistic species and a shepherd of biodiversity. I conclude that there is reasonable evidence to suggest pumas may play a vital role in driving community composition in the Bay Area. Thus, it might behoove managers to consider the species role in conservation more intently.

KEYWORDS

Mountain lion, diversity, coyote, mesopredator release, occupancy modeling

INTRODUCTION

The wildlife conservation actions of the 21st century must keep in mind a variety of conflicting priorities to ensure success given a rapidly changing climate and society. Ecosystems must be robust to more frequent disturbance, impacts of climate change must be considered in management plans, and land must often be allocated for multiple uses to simultaneously provide resources and preserve wildlife. Thus, to maintain ecosystem health and strength amidst these pressures, conservation efforts often manage landscapes for biodiversity and for preservation of historic species compositions and abundances (Hannah et al. 2002, Menéndez et al. 2006, Baugh et al. 2014). Biodiversity, a synthesis of numerous diversity metrics, such as species richness and abundance, is often a management priority as it is a salient indicator of ecosystem health and productive value to humans (Millenium Ecosystem Assessment 2010). On the other hand, managing for historic community compositions, and for particular species of ecological importance, can be vital to preventing an outbreak—or release—of a harmful species, maintaining resilience to disturbance, and preserving a breadth of economically and ecologically valuable species.

Interactions between organisms are essential to maintaining species composition, abundances, and, more generally, biodiversity. Community composition is determined by both “bottom-up” and, less accepted, “top-down” forces. The current paradigm emphasizes bottom-up forcing, which asserts that prey and nutrient availability determine which higher trophic tier species are found and how many (Laundré et al. 2014). However, top-down forcing has been observed in numerous studies, especially those oriented towards drastic changes in community compositions (Estes et al. 2011). Top-down forcing posits that the species and abundances are determined more heavily by organisms of trophic levels above them, often highlighting apex predators as influential on the their entire community. It is less clear the degree to which top-down forcing plays a role in driving community composition. Likewise, the mechanisms by which top-down forcing occurs are less accepted, despite being well established in literature (Estes et al. 2011). Through this study, I examine the general nature of this supposed top-down forcing, while also focusing on one mechanism in particular: mesopredator release. Mesopredator release describes the dramatic increase of mid-trophic level predator populations following the removal of apex predators. The temperate ecosystems of the Bay Area in

California present a similar community structure to other systems in which mesopredator release and trophic cascades in general have been observed.

The Bay is home to not only residential and agricultural development, but also the characteristic wildlife community seen in other studies of trophic cascades and mesopredator release. In systems regulated by top-down forcing and thus more subject to harmful trophic cascades, we often see a principal apex predator, a dominant ungulate herbivore, and a dominant mesopredator (Beschta 2003, Taylor et al. 2016). In city-adjacent natural areas in the Bay Area, the puma (*Puma concolor*), the mule deer (*Odocoileus hemionus*), and the coyote (*Canis latrans*), respectively, represent these roles. While pumas prey directly, and quite effectively, on deer, they typically are not engaged with killing coyotes. Interspecific competition, and the potential for harm that comes from kill site conflicts, is a more likely driver of coyote avoidance of pumas. Studies suggest that a “landscape of fear” generated by apex pumas on their prey and competitors explains differences in mesopredator coyote abundances and activity (Laundré et al. 2014). Thus, a lack of resources, the potential for harm, and reduced activity borne out of fear likely causes differences in coyote abundance and success based on spatial variation in puma presence. While suppressed coyote populations imply benefits for ranchers and urban residents alike, there are indirect effects of apex predator presence that may further impact community composition. Just as a change in puma populations may alter their prey and competitors, so will a change in coyotes populations impact their prey and other associated species. Therefore, in community composition studies of an apex predator and mesopredator, examination of indirect effects on an even lower tier of organisms may prove insightful.

This study aims to characterize the differences between two study areas with significantly different puma populations in order to assess how pumas may drive changes in community composition through top-down forcing. I hypothesized there exists an extensive apex predator influence exhibited both as direct influences on competitors and prey, and indirectly on the lower trophic level wildlife, including mesopredator prey and the local plant community, establishing the South Bay ecosystem as stable under “top-down” forcing. More specifically, influence of puma presence will limit the release of coyotes, incurring indirectly beneficial impacts for coyote prey. The North Bay ecosystem will not exhibit these biotic qualities to the same extent due to the lack of a strong *P. concolor* population. I hypothesized the North Bay, due to a minimal puma presence, will exhibit indicators of a trophic cascade that supported mesopredator release

and thus impacted abundances of mesopredator-associated prey. Finally, through these hypothesized mechanisms, I expect to observe greater biodiversity in the South Bay site.

METHODS

Study system

To study interactions between *P. concolor* presence and community characteristics, I relied on observed correlations between two study areas. Based on anecdotal accounts, the Marin Watershed (North Bay) study area has low puma presence and the San Mateo (South Bay) study area has high puma presence. Besides this key difference, study areas were selected based on their similarities to each other. Based on the best available data on their abiotic factors, I found these sites possessed similarities that would help limit confounding variables to consider in the analysis. The North Bay and South Bay study areas are free-water adjacent, within 10-15 miles of the coastline, and are primarily comprised of evergreen and mixed conifer forest. The South Bay study area is primarily below 100' elevation, while the North Bay study area ranges from below 100' to nearly 1000' elevation. The South and North Bay study areas receive 37 and 21 inches of rainfall on average per year, respectively. Figure 1 depicts the study system discussed.

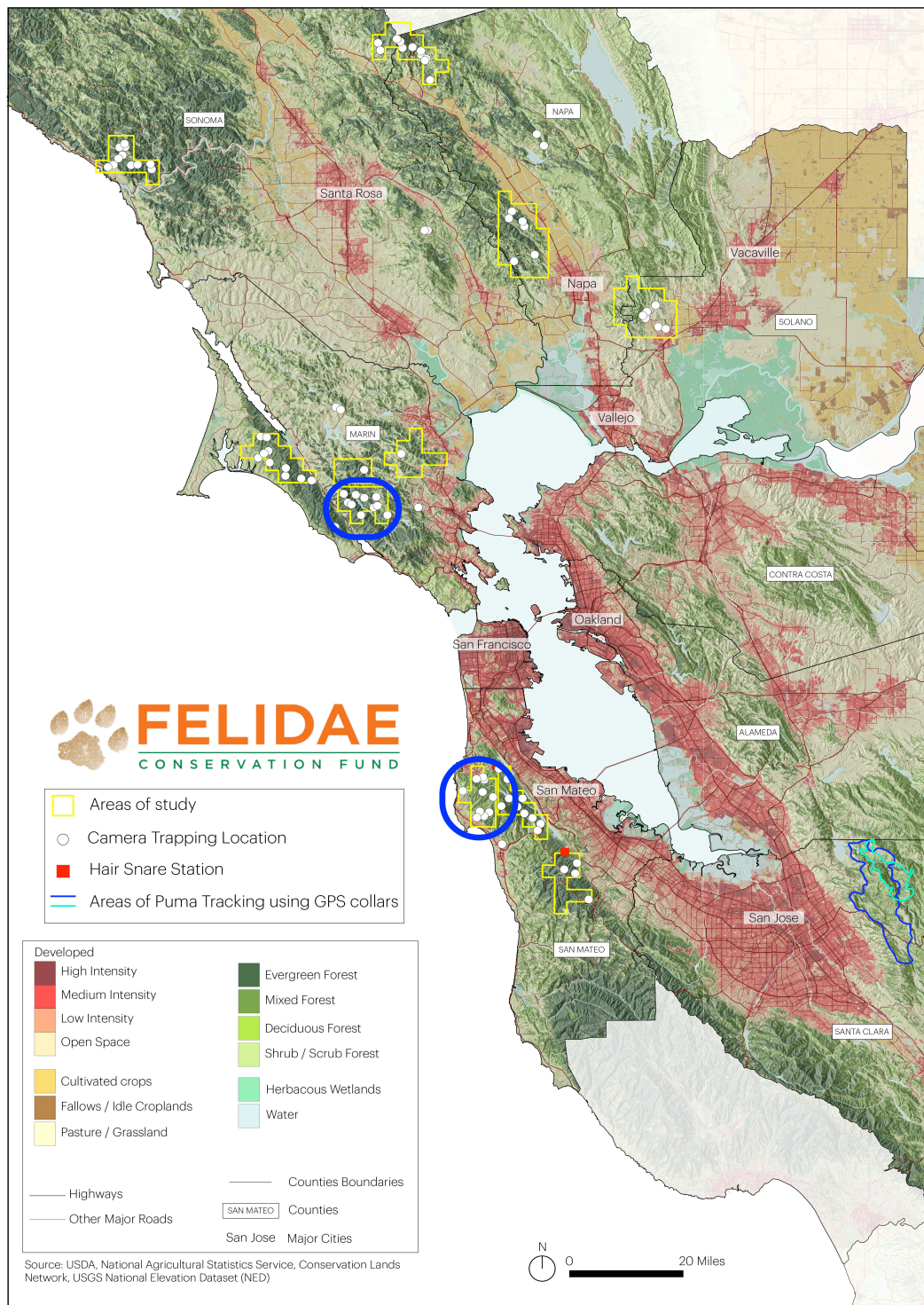


Figure 1: Study site locations. North Bay study area cameras (depicted by the higher circle) are located within the Marin Municipal Watershed District. South Bay study area cameras (depicted by the lower circle) are located within the San Francisco Public Utilities Commission reserve near San Mateo, CA.

Data collection methods

Camera trapping

To properly perform a comprehensive assessment of both ecosystem locations, I executed a variety of measurements at three trophic tiers. I employed the use of 10 Felidae Conservation Fund (Bay Area Puma Project) camera traps at each study area to collect a representative sample of photos of the animal community. Cameras were located on or near rugged (usually unpaved) roads, as many mammals, especially puma, use roads opportunistically for expedited movement (Rich et al. 2017). Locations were determined and established previously by the Felidae Conservation Fund for optimal wildlife interaction and minimized autocorrelation between traps locations. Camera trap data was then processed and delivered to me with animals seen categorized in a Microsoft Excel spreadsheet. I reorganized this data to calculate coyote occupancy, relative activity and presence of other mammals, and diversity metrics, all explained later. Because ensuring as much consistency as possible in ecological studies is vital, I only used camera trap data from September 2016-March 2017 and performed field assessments during the same months the following year to account for seasonality. Additionally, I ensured data used for this study was a part of a continuous stream of data to limit bias and sample size inaccuracies in the analysis. However, analysis was not limited to data collected from camera traps.

Habitat assessment

I performed habitat assessments following a strict protocol to compensate for limitations in camera trapping and to characterize each site's habitat. I checked each camera trap site once during the data collection period of September 2017-March 2018. Around each camera trap, I established a fixed 15m radius circular plot and conducted surveys of the encircled biota. I surveyed each camera site for five minutes for animal sign, including but not limited to scat, calls/songs, nest indication, and direct observation. Any wild animals utilizing the sampled circular plot were recorded for the purposes of species richness calculations. Vegetation surveys focused less on species identification (excluding tree species identification) and more on characterization of the plant community structure. I recorded percent groundcover by using 1m²

quadrats at 4 predetermined locations per site (10m North, South, East, and West of the plot center) by identifying the plant or ground cover type (water, bare/rock, duff/downed woody debris, grass, leafy/forb, fern, or shrub). For each tree in these circular plots, I noted species and diameter at breast height (DBH) to later calculate basal area. DBH is calculated using a D-tape. In the plots, I also recorded canopy cover using a vertical sighting tube (a form of densitometer) at 13 locations at each site (5m, 10m, and 15m North, South, East, and West from plot center, and at the plot center itself).

Data analysis methods

With respect to the animal community analysis, I analyzed camera trap data of pumas, coyote, and several other prey species such as deer and small mammals, among others. In order to estimate study area diversity, I used camera trap data to assess the presence and frequency of sightings of any terrestrial vertebrate species (including mammals, non-avian reptiles, amphibians, and birds). I recorded all vertebrate species and sign seen on camera and during habitat assessments to determine species richness of each study area. I used the number of camera sightings in lieu of each species' abundance for the calculation of a Shannon diversity index. The Shannon diversity index is an effective metric to summarize study area biodiversity, and weights rare species like pumas more heavily than other indices do. It is important to note that sightings are not an accurate indicator of abundance, as some species are more mobile and conspicuous, meaning they would appear more frequently on cameras. However, as this study is concerned not just with population sizes but behavioral responses of prey to predator presence, relative activity (represented well by camera sightings) between study areas is a valuable metric. Additionally, I have no reason to believe the manner by which species are captured on camera is any different between study areas. These analyses provided an understanding of study area diversity and species activity. However, further analysis was necessary to ascertain the occupancy of coyotes, which literature suggests may exert strong ecological pressures on certain members of the community (Ripple et al. 2013).

Occupancy modeling

Occupancy modeling was an essential portion to this study's analysis. I employed occupancy modeling to indirectly quantify the relative probability that a coyote is influencing the community's composition. Modeling was performed in R using the {unmarked} package, and used data from the study's sampling period (September 1st-March 8). Using occupancy modeling, I was able to use the frequency of coyote sightings to assert the probability that the species occupied that area, and thus could be considered influential in shaping the camera habitat's ecology. To test the coyote populations' occupancy, we used a week as a detection time range. If a coyote appeared on any camera trap within the week, the probability that coyotes occupy the area would increase. Coyote occupancy is then compared against covariates such as plant measurements to identify any significant correlations. The plant covariate "leafy/forb" represents the most desirable forage for the local mule deer populations, and thus was chosen as the plant covariate most representative of deer activity. I standardized covariates so they possessed means of 0 and standard deviations of 1. This allowed for less complicated analysis of relative differences between study areas. However, as occupancy modeling is species specific, I instead used statistical tests to analyze the effects of coyote occupancy on the diversity of the small mammal community.

Small mammal diversity

I quantified small mammal diversity by comparing the relative activity of the small mammal community on the camera traps. It is important to investigate small mammal diversity because much of the California faunal diversity is found within the small mammal community, and thus provides us an important look into the potential effects of coyotes on community diversity. I assumed the relative activity of small mammals on camera traps would be an effective proxy for small mammal diversity because a suppressed small mammal community would not only be less abundant, but also likely be less well adapted to inconspicuously avoid detection (by coyotes or cameras). Thus, the relative activity of small mammals can be used to assess the impact of coyote occupancy on the community and diversity of captured small mammals. I computed a two-sample, unpaired t-test to compare the mean activity levels between

study areas. I also used a histogram to represent the number of sites at which small mammals exhibited each standardized activity index.

RESULTS

Study site

In total, we recorded 78,942 animal sightings from both the North Bay and South Bay study areas between 2012 and 2017 using Felidae Conservation Fund camera traps. As stated, this study concerns only a portion of these data, between September 2016 and March 2017. *Puma concolor*, the focal species of this study, was captured 1,442 times by South Bay cameras, and 3 times by North Bay cameras. Regarding comparisons of study area diversity, calculations of species richness and Shannon diversity indices indicate the South Bay possesses greater biodiversity. I detected 24 species at the South Bay study area and 20 species at the North Bay study area, indicating the South Bay has slightly greater species richness. However, the Shannon diversity index of the South Bay community ($H = 1.44$) is notably greater than the index of the North Bay community ($H = 0.78$). Tables 1 and 2 depict the results of the diversity portion of the analysis.

Table 1: North Bay study area community diversity. Data were processed from Felidae Conservation Fund camera traps.

North Bay				
Species	Total Sightings	Proportion of Total	$Pi*lnPi$	Shannon Index
Black-tailed (mule) Deer	1449	0.797907489	-0.18	0.782057268
Bobcat	30	0.016519824	-0.068	
Brush Rabbit	33	0.018171806	-0.073	
Coyote	170	0.093612335	-0.222	
Grey Fox	107	0.058920705	-0.167	
Northern Raccoon	21	0.011563877	-0.052	
Puma	3	0.001651982	-0.011	
Squirrel - unknown species	3	0.001651982	-0.011	

Table 2: South Bay study area community diversity. Data were processed from Felidae Conservation Fund camera traps.

South Bay				
Species	Total Sightings	Proportion of Total	$P_i \ln P_i$	Shannon Index
Bird - Unknown Species	3	0.000963701	-0.007	1.438841247
Black-tailed (mule) Deer	1755	0.563764857	-0.323	
Bobcat	109	0.035014456	-0.117	
Brush Rabbit	3	0.000963701	-0.007	
California Quail	6	0.001927401	-0.012	
Coyote	40	0.012849341	-0.056	
Desert Cottontail	2	0.000642467	-0.005	
Grey Fox	448	0.143912624	-0.279	
Mouse - Unknown Species	3	0.000963701	-0.007	
Northern Raccoon	31	0.00995824	-0.046	
Puma	414	0.132990684	-0.268	
Rat - Unknown Species	19	0.006103437	-0.031	
Squirrel - unknown species	53	0.017025377	-0.069	
Striped Skunk	208	0.066816576	-0.181	
Virginia Opossum	19	0.006103437	-0.031	

Occupancy modeling

Occupancy modeling was used primarily to ascertain the probability of coyotes occupying a given site at each study area. Using the {unmarked} package in R, I calculated an occupancy probability of 0.816 in the North Bay and an occupancy probability of 0.704 in the South Bay (Table 3). Detection probability of coyotes in the South Bay was .0684, lower than the 0.136 probability in the North Bay (Table 3). I also used the model to investigate potential relationships between coyote occupancy and the desirable forage (leafy/forb) covariate, as discussed. I found no significant relationship between coyote occupancy and the forage covariate in the North Bay (estimate = $1.71e^{-7}$). However, in the South Bay, I found a negative relationship between coyote occupancy and the forage covariate (estimate = -0.777). However, no other significant relationships were found with respect to plant and habitat variables.

Table 3: Occupancy and detection probabilities for coyote by study site. Values were derived from R {unmarked} analysis of Felidae Conservation Fund camera trap data.

Coyote Occupancy		
Coyote (<i>Canis latrans</i>)	South Bay	North Bay
Occupancy Probability	0.704	0.816
Detection Probability	0.0684	0.136

Small mammal diversity

In order to best understand the effects of mesopredator occupancy on the small mammal community, I analyzed the relative activity of 8 photographed small mammal species/genus characteristic of coyote mammal prey (Ripple et al. 2013). These included black-tailed jackrabbit, brush rabbit, desert cottontail, eastern grey squirrel, other squirrel species, Merriam's chipmunk, *Mus spp.* (mouse), and *Rattus spp.* (rat). In comparing relative activity of the study area communities, I found that the South Bay shows a more active small mammal community with a mean activity index of 0.44, compared to the North Bay activity index of -0.46. As these values and Figure 2 suggest, the small mammal community of the South Bay site is captured more frequently on camera, on average.

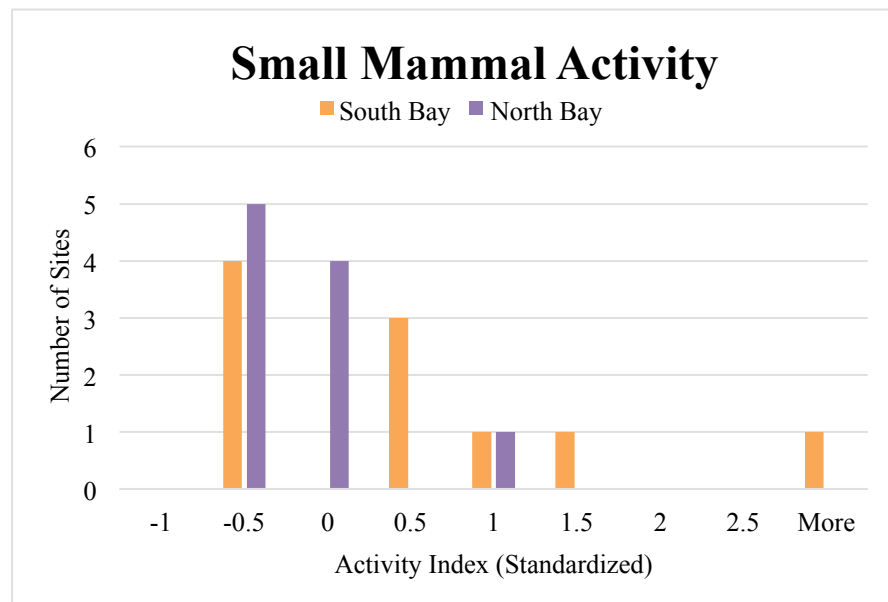


Figure 2: Histogram of small mammal activity between study areas. Activity was derived from frequency of sightings on Felidae Conservation Fund camera traps. Small mammal activity is a proxy for diversity within the small mammal community.

DISCUSSION

Compared to the North Bay, I found a greater presence of pumas, a lower probability of coyote occupancy, and greater small mammal activity in the South Bay. Evidently, there exists a severe disparity in puma presence between the two study areas. Studies suggest removal of an apex predator such as *Puma concolor* may lead to a trophic cascade, impelling changes in species found and their abundances (Beschta 2003, Estes et al. 2011). This study system served as an effective medium to investigate this possibility due to the stark difference in puma populations. If we can reasonably assert a species occupies a study area, we can then assume said species could effectively influence the ecology of the study area. Therefore, the South Bay, possessing a lower probability of coyote occupancy, would experience the effects of coyote occupancy to a lesser degree than the North Bay. Greater small mammal activity on South Bay camera traps denotes less repressed small mammal communities. Finally, the South Bay, based on calculations of species richness and Shannon indices, is more biodiverse with respect to its fauna. The synthesis of these results paints a picture of a less diverse North Bay study area impacted by a mild mesopredator release. These findings suggest top-down forcing may be a significant driver of community composition in this study system.

Biodiversity

The South Bay possesses both a strong puma population and nearly twice the Shannon diversity index value of the North Bay. Though the difference between the study areas' species richness was not particularly great, it corroborates the hypothesis that the Shannon index supports; a robust apex predator population benefits their ecosystem's biodiversity. This finding on its own is helpful in managing for diverse wildlife communities. However, the question of how apex predators—in this case, pumas—drive community composition cannot be answered by diversity metrics alone. While this finding is an important datum to our assertion that apex predators contribute to shaping community composition, the other findings of this study help inform the question of how pumas influence their proximate biota. Indeed, the most significant finding came not from the diversity portion of this study, but from the examination of mesopredator release and its impacts.

Mesopredator Release

When investigating how apex predators impact their ecosystems, examination of smaller, yet often more opportunistic mesopredators is essential. It is for this reason that this study's analysis of pumas looked intently into coyote ecology, not just as a response variable to puma presence, but also as a mechanism by which the rest of the ecosystem can be impacted. Though high in both study areas, the occupancy and detection probability of coyotes in the North Bay was higher than that of the South Bay. Importantly, coyotes are habitat generalists and, like many other mesopredators, are capable of opportunistically persisting despite inhibiting factors, such as competition with more dangerous predators (Ripple et al. 2013). So, while the occupancy probability of 0.704 in the South Bay is high, this can be attributed to the coyote capability of tolerating less than ideal conditions. In fact, observations of coyotes effectively thriving in a variety of habitat qualities suggest that pumas are instead limiting coyote occupancy through a landscape of fear (Laundré et al. 2014). The North Bay occupancy probability of 0.816 is markedly greater, indicating the North Bay in some manner suits coyotes better than the South Bay. The strong relationship between a significantly lower puma presence and this higher occupancy probability is indicative of a lack of puma-induced fear experienced by the North Bay coyotes. Additionally, the relationships between this difference in coyote occupancy and other community facets between study areas garner support for the notion of mesopredator release. A change in mesopredator populations triggered by a reduced apex predator presence has been seen to cause community composition changes similar to those seen in this study (Taylor et al. 2016).

An observed difference in coyote occupancy between study areas coincides with significant differences in recorded flora and fauna. I have observed relationships between small mammal diversity and deer forage that I assert act as symptoms of a mesopredator release in the North Bay, where pumas are far less present. I found a significant difference in small mammal activity between the sites, with the South Bay presenting both more sightings and photographed species. This indicates greater species richness, abundances, and general activity in sites with lower coyote occupancy. These parameters portray the South Bay as a site with greater small mammal diversity. The inverse correlation (estimate = -0.777) between coyote occupancy and the desirable deer forage covariate in the South Bay suggests that sites where pumas exclude coyotes will also have less deer, and thus more forage that would otherwise be consumed by the

browsers. These findings corroborate my literature-supported hypothesis that pumas will regulate ungulate herbivore populations more than coyotes. Coyotes often experience population growth alongside deer and focus less on deer depredation due to their generalist diet (Ripple et al. 2013). Therefore, coyote suppression by pumas suggests that deer populations are more controlled in the South Bay.

Ultimately, I have found evidence suggestive of top-down forcing by pumas on the South Bay vertebrate community. The observed high presence of pumas induces behavioral changes to their most prolific competitor, the coyote (Laundré et al. 2014). Coyotes are thus more likely to occupy sites where pumas are less present. Coyotes, as effective and opportunistic predators, consume a variety of small mammal species, which yields a less active and less diverse community of small mammals, the taxa that contains the most diversity in these ecosystems. The described trophic cascade is portrayed in Figure 3, omitting deer, as they were not directly observed.

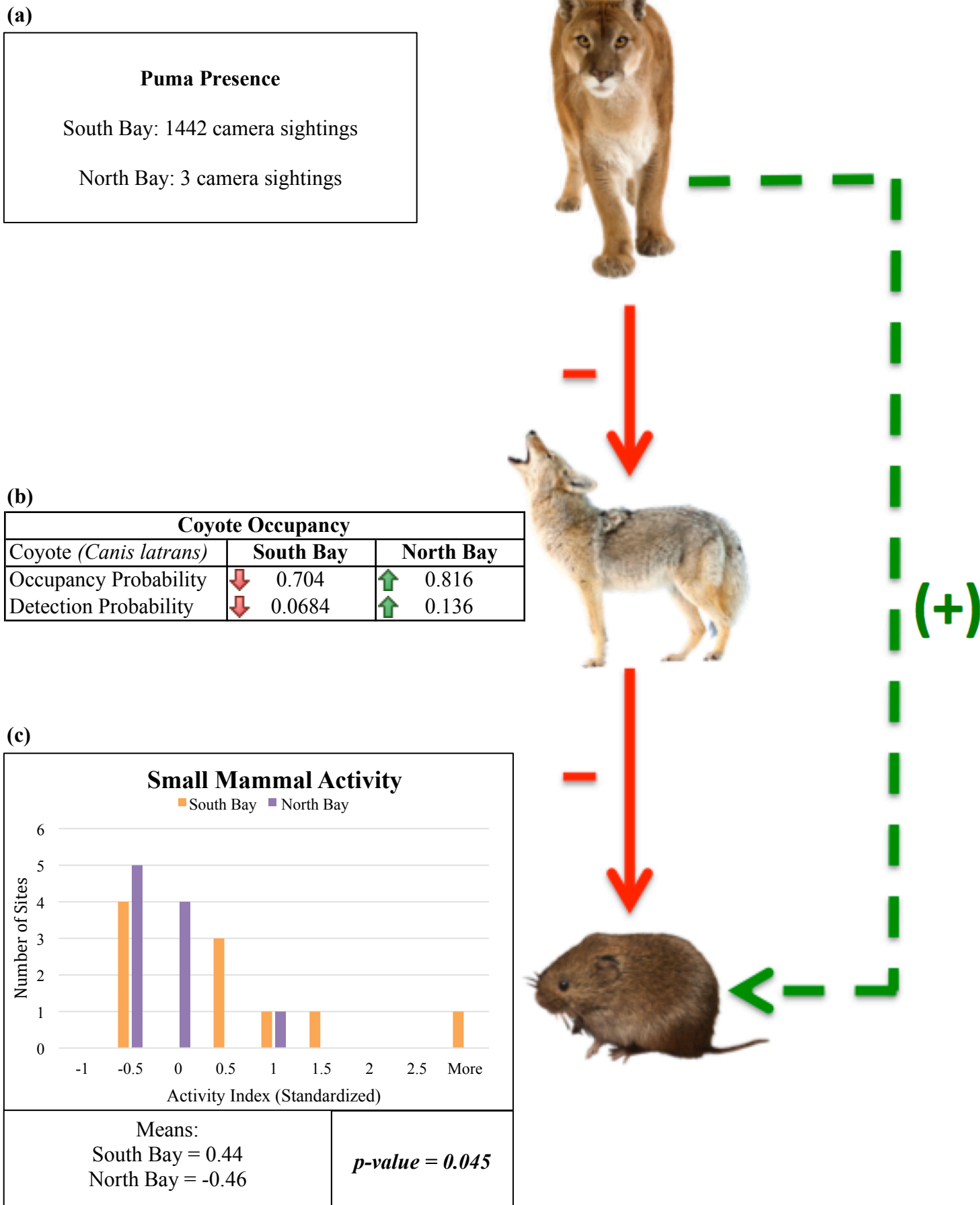


Figure 3: Hypothesized South Bay top-down forcing with supported findings: The hypothesized interactions are supported by (a) a higher puma presence, (b) lower coyote occupancy, and (c) greater activity within the small mammal community. Data was sourced from the Felidae Conservation Fund.

Though I was unable to incorporate deer occupancy and activity into this study, we can make some literature-supported inferences on the deer community based on puma presence and deer forage. Principally, the landscape of fear is not exclusive to coyotes. Medium and large bodied prey, such as mule deer, have been observed to be extremely susceptible not only to puma predation but puma fear effects (Breviglieri et al. 2017). Though difficult to quantify given the limitations of this study, I posit that differing population sizes and activity levels of deer due to puma predation and fear effects may be driving significant differences in plant community characteristics, given that deer are the most dominant herbivore in these areas (Estes et al. 2011). Future studies could examine particular indicators of deer overbrowsing seen in other studies, such as sapling elimination and species composition shifts (Beschta 2003, Estes et al. 2011). The North Bay, experiencing less puma influence, would likely exhibit some of these differences.

Limitations and Future Directions

There are several areas in which this preliminary study can be used to delve into the discussed ecological interactions. Due to the wide scope of this study, I was limited in my ability to tackle additional analyses that may prove interesting or academically valuable. Each segment of the greater study required too much fundamental effort to expend time diving deeper without sacrificing another desired section. More in-depth studies can be derived from this broad ranging, interdisciplinary thesis if the study's question focused on an individual section or a more specific hypothesis. For instance, in the future, one could examine deer behavior, which may be a good indicator of deer fitness, the potential of deer to overbrowse, and the degree to which fear impresses upon a landscape. Another obstacle lied with the difficulty of measuring faunal diversity. Small mammals were more difficult to detect given the equipment and methods utilized. In future studies, I would employ the use of Sherman traps to assess small mammal species richness more accurately.

The wide scope of this study also left only so much effort available to investigating potential drivers of community composition. Thus, because my central research question pertained more to biota, especially the vertebrate community, I was unable to incorporate the potential abiotic effects that may also drive community composition. Though physical factors were considered when selecting study areas, I opted to omit measurements of other factors such

as site-specific elevation or soil quality. I measured plants during field assessments to account in part for environmental factors, and found these not statistically significant, with the exception of deer forage. Future studies that narrow the objective may be able to redistribute more time towards checking for these sources of potential bias.

Broader Implications

Based on the data collected and models run, I assert that it is reasonable to posit that community diversity and composition was driven greatly by pumas through top-down forcing. Though context is very important and no system is exactly the same, these findings imply similar drivers of community composition may exist in analogous communities. The studied community consisted of one primary apex predator (*Puma concolor*), a prolific mesopredator (*Canis latrans*), and a dominant, large browser species (*Odocoileus hemionus*) acting as the most influential herbivore on the landscape. In systems similar to these—of which there are many—we might see similar top-down forcing. Thus, to the Bay Area, to adjacent landscapes, and to comparable ecosystems, conservation of pumas can be vital, and ultimately ease the difficulty of planning for biodiversity and managing wide-ranging mesopredator populations.

One of the aims of this study was to contribute to the literature on top-down forcing, trophic cascades, and mesopredator release. It is indeed humbling to see evidence of this in ecosystems so near to the Bay Area. However, it is also essential to remember that these systems and interactions are complex, and do not translate perfectly between habitats. For example, Levi and Wilmers (2012) observed how coyote populations can benefit small mammal diversity, rather than suppress it as I have seen in the North Bay. So while this study supports the theory of top-down forcing, it also is an important reminder that ecology is more complex than our desire to categorize often purports. For any given habitat being managed, site-specific ecological research is paramount. As we examine these systems more, we quickly realize that bottom-up forcing is not the sole mechanism, that community ecology is complex, and that conserving wildlife interactions has cascading benefits for humanity and nature alike.

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