



# OPEN Impacts of coyote colonization on coastal mammalian predators

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Extreme ecosystem modification by humans has caused drastic reductions in populations and ranges of top mammalian predators, while simultaneously allowing synanthropic mesopredator species to expand. These conditions often result in inflated local densities of highly adaptable mesopredators that disrupt trophic dynamics and place unsustainable predation pressure on native prey populations. Colonization of a dominant predator may lead to top-down control of mesopredators and restore trophic balance. Coyotes are a novel colonizer of some coastal barrier islands of eastern North America, offering an opportunity to test how the addition of an apex predator impacts an established guild of mesopredators. To assess their trophic impact, we conducted 75,576 camera trapping hours over an 18-month study period, capturing > 1.5 million images across 108 coastal camera sites. Using two-species occupancy and habitat use models, we found sizeable effects of coyote habitat use on that of red foxes and free-ranging domestic cats, suggesting that coyotes function as apex predators in barrier island ecosystems. In fact, the only factor that determined the spatial pattern of highly ubiquitous red foxes was the sympatric habitat use of the largest carnivore in the food web—coyotes. That 'novel' apex predators can become established in coastal food webs illustrates the highly dynamic nature of conservation challenges for habitats and species at the edge of the sea.

**Keywords** Sandy beaches, Camera trap, Coastal food webs, Mesopredator release, Top-down control, Apex predators

Global expansion of human populations and the parallel loss of natural habitat cause widescale adverse effects on wildlife, particularly apex predators<sup>1,2</sup>. Historically viewed as pests, apex predators have been subjected to intensive lethal controls, including intended eradication objectives<sup>3,4</sup>. Such destructive measures were the focus of entire governmental organizations in North America in the 19th and early twentieth centuries<sup>5,6</sup>, are still encouraged by bounties in many localities across the globe<sup>7</sup>, and are typically viewed as necessary to sustain animal husbandry<sup>8,9</sup>. These centuries-long trends have reduced populations and contracted the ranges of many large carnivores globally<sup>10,11</sup>. In addition to direct killing, habitat loss and degradation contribute to apex predator declines, mainly by compressing available habitat and prey<sup>10,12,13</sup>. Further, human disturbance can create noticeable behavioral shifts in predatory species (i.e., increased nocturnality in brown bears (*Ursus arctos*) during hunting seasons<sup>14</sup>; trail avoidance by bobcats (*Lynx rufus*) during increased times of human use<sup>15</sup>).

Areas where apex predator populations have been extirpated or significantly reduced can experience loss of top-down trophic regulation<sup>16,17</sup>, leading to several downstream impacts on biodiversity and ecological functioning. For example, the absence of large carnivores across several ecosystems has led to inflated populations of large herbivores and thus, unsustainable levels of herbivory<sup>17,18</sup>. Excessive herbivory, in turn, reduces the total primary productivity of affected ecosystems and alters habitat quality for resident taxa<sup>19–21</sup>. Loss of aboveground biomass can also reduce the carbon storage capacity of ecosystems<sup>22</sup>, ultimately contributing to the elevated atmospheric carbon dioxide levels<sup>23,24</sup>.

Apex predator loss also significantly impacts lower-ranking predators by removing the regulatory effects of intraguild predation and competition<sup>7,25–28</sup>. Such “mesopredator release”<sup>27</sup> causes populations of smaller predators to persist at much higher densities and expand into previously unoccupied areas<sup>7,26,29</sup>. Mesopredator release leads to intense predation pressure on smaller prey species and can have lasting effects on many species of conservation concern<sup>30–33</sup>. For example, in the American West, coyote (*Canis latrans*) populations have risen in response to the extirpation of gray wolves (*Canis lupus*), leading to population and harvest declines in many leporid species native to the region<sup>34</sup>.

In coastal ecosystems, mesopredators are now an abundant and broadly impactful component of the trophic web due to the loss of historical apex predators from these areas<sup>35–38</sup>, such as the gray wolf and black bear (*Ursus*

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*americanus*)<sup>39</sup>. They frequently cause high prey mortality across all life stages of several endemic and threatened species<sup>40–43</sup>. Because coastal mesopredators are also proficient synanthropes, capable of thriving in or near human-dominated areas, their populations are not regulated by the asynchronous dynamics of marine-derived resource pulses<sup>44</sup>. Instead, coastal mesopredators are continuously supported by human food subsidies sourced from adjacent development<sup>45–48</sup>. Mesopredator population vitality and the relentless predation pressure they place on prey species make them arguably one of the most intractable problems for coastal biodiversity conservation, and they are often the targets of intensive management intervention<sup>31,32,36,49</sup>.

In the past century<sup>50</sup>, coyotes have expanded their geographic range significantly and are now colonizing ocean-exposed sandy beach ecosystems<sup>51–53</sup>, presenting an opportunity to examine the potential for restored trophic regulation. Coyotes present an interesting example of a species wavering between the status of an apex predator and a carnivore more ‘typical’ of a mesopredator. Coyotes serve as apex predators in some ecosystems<sup>27,54,55</sup>. However, they have also been considered members of the mesopredator guild when sympatric with larger carnivores<sup>55,56</sup>. Especially in eastern North America where their presence is most novel, the functional niche of coyotes within beach ecosystems is still unclear due to their plasticity in behavior and ability to persist in areas of human disturbance<sup>57–59</sup>. Within beach ecosystems of eastern North America, there is no large carnivore to supersede novel coyotes<sup>39,51</sup>, which may allow them to dominate the predator guild historically found in these areas<sup>55</sup>. Studies in other systems have shown that coyotes can impact habitat use of mesopredators through top-down control<sup>27,54,60</sup>, but these impacts are not uniform across different habitats<sup>61</sup> or mesopredators communities<sup>62,63</sup>. Ocean-exposed coastal areas are comprised of a mosaic of highly urbanized landscapes interspersed with natural areas<sup>40,64,65</sup>, leading to uncertainty in the trophic role coyotes serve within coastal predator communities.

Here, we examined the potential for coyotes to function as apex predators within ocean-exposed sandy beach ecosystems. We focused on how coyote habitat use affects the distribution and activity of co-occurring mesopredators. We used an 18-month camera trapping effort to document the habitat use of mesopredators in a sandy beach coastal system and test for shifts in species-specific habitat use resulting from coyote presence. We hypothesized that areas supporting coyotes would be used less by mesopredators historically found in these ecosystems, suggesting a modification of predator dynamics in coastal food webs.

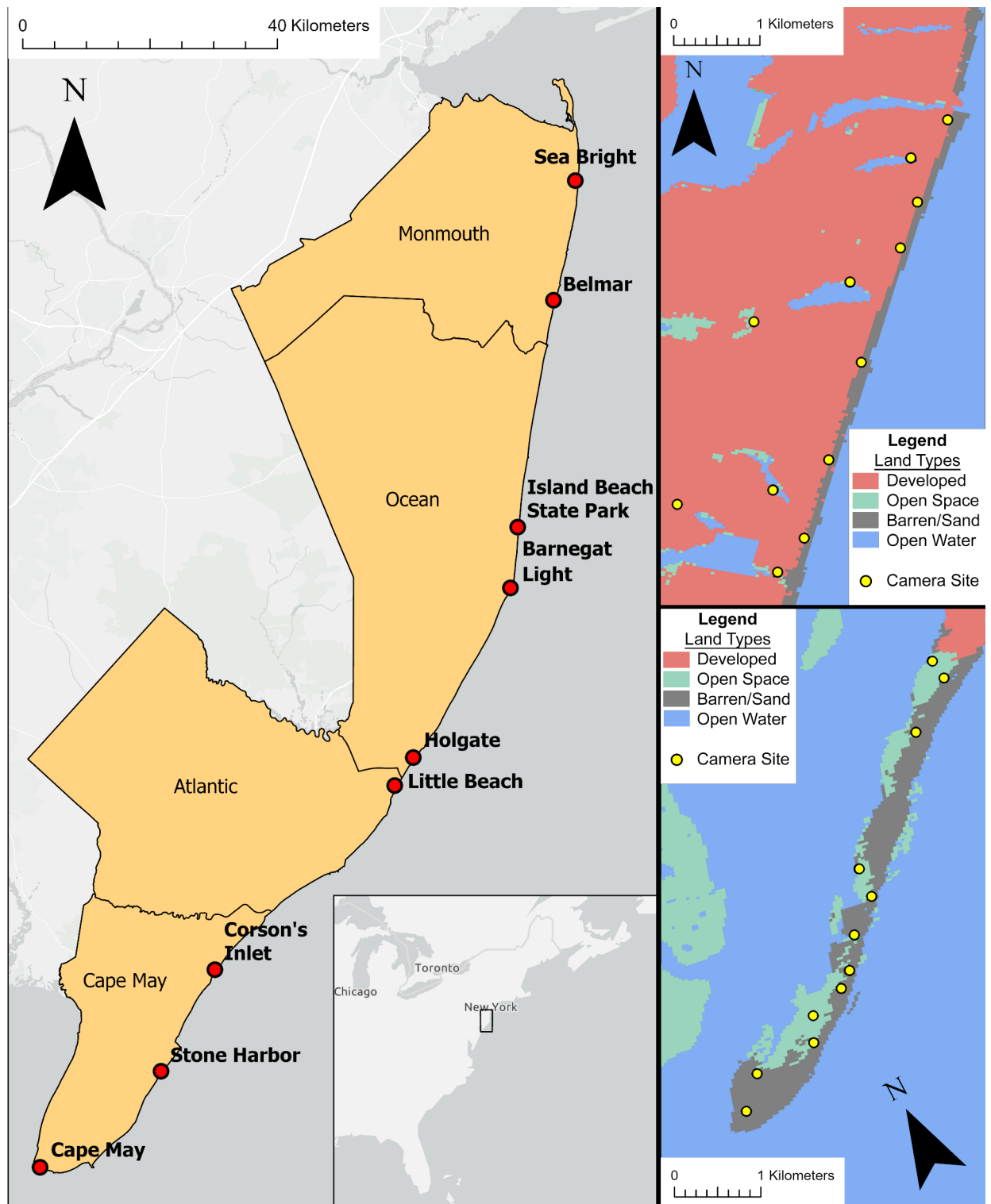
## Methods

### Study area

Our study area encompassed 200 km of the New Jersey (USA) coastline, extending from the Borough of Sea Bright (Monmouth County) in the north to Cape May Point in the south (Cape May County; Fig. 1a). We monitored carnivore presence and activity within coastal habitats across nine study sites ranging from 350 to 1250 hectares and spanning a gradient of heavily urbanized localities to undeveloped, federally preserved land. The study area is one of recent coyote expansion. Records indicate coyotes were uncommon in much of our study area during the timeframe of our sampling<sup>52,66</sup>, making it an ideal area to test how their presence impacts the use of other mesopredators. Within each study site, we established 12 camera locations, separated by at least 400 m. Based upon the published home range size of our target taxa<sup>67–69</sup>, this inter-camera distance makes it reasonable to treat each location as an independent sample of the resident carnivore community.

### Surveying coastal predators

We focused on the free-roaming mammalian predators typically found in coastal ecosystems along the mid-Atlantic coastline of the United States. Sites were monitored in non-overlapping 12-month windows, with the first five study sites being monitored from April 2019 to March 2020, and the last four study sites being monitored from September 2019 to August 2020. At the start of the field survey, we randomly selected four camera locations within each site and deployed a single Reconyx Hyperfire HP2X Pro (Reconyx Wildlife Cameras, Holmen, Wisconsin, USA) infrared camera for a period of 28 days. We simultaneously monitored four camera locations per site. To cover more area and more diverse habitats within each study site, we rotated cameras among 12 camera locations within each study site (Fig. 1), resulting in 108 unique camera locations across our study area. We mounted cameras either onto a stake or existing wooden post or tree ~80 cm above the ground and directed them at an ~45° angle downward to obtain a field of view of ~1 m out from the base of the camera mount<sup>70</sup>. We set camera motion triggers to high sensitivity and programmed each camera to capture a set of five pictures at three-second intervals once triggered. To increase the likelihood that a predator in the area would walk past our camera<sup>71</sup>, we deployed three attractants to each camera station at the start of each survey period. Visual bait consisted of canned sardines (224 g). Scent lures included two 2-g pieces of untreated lambswool, one soaked in ~5 mL of ‘Caven’s Gusto’ (Caven’s Quality Animal Lures, Wisconsin, USA), and the other in ~5 mL of Shellfish Essence Oil (F&T Fur Harvesting Trading Post, Michigan, USA). Both pieces of lure-soaked lambswool were placed in two side-by-side 3–5 cm divots dug into the substrate (i.e., sand or loamy soil) 1 m directly in front of the camera mount and covered with shells to reduce their exposure to rainfall. At the end of the 28-day survey period, we moved each of the four cameras to a new location within the study site, using a random selection without replacement procedure. When all camera locations within a study site had been surveyed once, we began the selection process anew, randomly selecting four camera locations without replacement from the sampling pool of the eight unoccupied camera locations available at the end of each survey period. We manually viewed every image recorded and defined a species as being present at a camera location if it appeared in one image during the survey period.



**Figure 1.** (a) Study area, encompassing > 200 km of the coastline of New Jersey, USA from 2019 to 2020. Polygons represent coastal counties of New Jersey. The nine study localities are shown as red points. (b) Camera sites located within Belmar, a heavily developed locality in which no coyotes were detected, overlaid onto a land use cover layer. (c) Camera sites located within Holgate, a federal preserve where 32% of our coyote detections occurred, overlaid onto a land use cover layer. Layer data for panels b and c is from the USGS National Land Cover Database, 2019 and the maps for panels a, b, and c were generated using ArcGIS Pro 2.7.0 <https://www.esri.com/arcgis>.

### Factors influencing detectability and habitat use of coastal predators

At each camera location, we tested five predictors hypothesized to influence our ability to detect mammalian predators. From the LANDFIRE GIS database, which classifies vegetation fuel stores across North America using satellite imagery<sup>72,73</sup>, we calculated both the percent cover of vegetation  $\geq 50$  cm in height within a 30-m radius of each camera location, as well as the distance from each camera site to the closest patch of vegetation  $\geq 50$  cm in height<sup>56,74,75</sup>. To incorporate the relative importance of resources (i.e. food subsidies, refugia) from human-modified landscapes<sup>29,58,75,76</sup>, we measured the distance to developed land as designated by the United States National Land Cover Database<sup>77,78</sup>. Because our focal species' peak activity times range from crepuscular to nocturnal, and most of the activity on our cameras occurred at night<sup>56,74,79</sup>, we accounted for the seasonal change in day length (photoperiod) at each camera location by assigning the photoperiod of the 14th day of each 28-day survey. Because each study site was monitored over 12 months and the photoperiod value was different for each month, this covariate also allowed detection estimates to vary between each survey period. Most of our focal species exhibit similar life histories, with heightened levels of movement in spring (breeding and rearing activities) and early fall (dispersal<sup>80–82</sup>). Therefore, we squared the photoperiod values to account for the possibility that the relationship between detection probability and photoperiod may be nonlinear (i.e., detection probability may peak near the equinoxes) and included the linear version of photoperiod within these models as appropriate. Finally, because coastal areas in the United States are relatively more populated between late May through early September (coinciding with the summer holiday), we captured potential seasonal fluctuations in availability of human subsidies using a binary covariate to designate survey months falling within this timeframe.

We also tested six predictors we hypothesized might affect carnivore habitat use, including distance to development and distance to vegetation, as described above, as well as distance to the mean high tide line, distance to marshland, small prey activity, and human population density. Because our focal taxa exhibit different sized home ranges, we focused on the proximity of resources to camera locations, and thus the areas of known use for our focal taxa, rather than testing for differing scales of importance for each of our focal taxa. Coastal carnivores rely upon multiple food resources, including both pulse carrion strandings from the marine environment, as well as rodent, lagomorph, and mussel prey<sup>69,83–86</sup>. To capture proximity to aquatic food resources, we measured the Euclidean distance from each camera location to the mean high-water line using a GIS layer of New Jersey Tidelands<sup>87</sup>. In addition, we quantified the Euclidean distance to the nearest marshland using the United States Fish and Wildlife Service Wetlands Inventory<sup>88</sup>. We also used the combined count of unique occurrences of both rodents and lagomorphs at each of our cameras to capture terrestrial prey availability<sup>56,89–91</sup>. Finally, we considered how human disturbance might affect our focal species' use of coastal habitats by overlaying a 1-km resolution world population data layer<sup>92</sup> onto our study area and recording the population value of the square kilometer in which each camera was located. All remotely sensed data were processed from sources updated between 2019 and 2020 using ArcGIS Pro 2.7.0<sup>93</sup> at a 30-m resolution unless otherwise noted.

### Modeling carnivore detection, use, and interactions

We incorporated the presence/absence data extracted from camera traps into a three-step occupancy modeling approach to evaluate detectability, habitat use, and interspecific interactions. Our steps were to: (1) identify the important detection variables for each focal species; (2) include those in a second step aimed at identifying important variables for occupancy; and (3) incorporate both results into two-species detection histories to identify species co-occurrence trends. Generating results in this stepwise fashion reduces the overall number of competing models within a single candidate set and allows for a clearer understanding of how each putative predictor influences detectability and habitat use<sup>94–96</sup>. To estimate occupancy, models must assume site closure (i.e. if a species is seen once at a site, it is assumed that it is always present at that site<sup>97</sup>). However, the species we modelled are highly mobile<sup>68,98–101</sup> and likely to move into or out of our study area throughout the 12-month monitoring period. Therefore, we consider the *probability of occupancy* as the *probability of habitat use* by a species<sup>102</sup>. We normalized all predictors by subtracting the standard deviation from each value and then dividing by the mean of each respective covariate<sup>103</sup>. Before generating candidate model sets, we checked for correlations among predictors and found that all pairwise correlation coefficients were independent (Pearson's  $r < 0.5$ )<sup>104</sup>.

We first estimated detection probabilities by generating a set of 32 single-species, single-season occupancy models to test various combinations of the five candidate detection predictor variables (models listed in Supplemental Information, Table S2). We ranked competing models using the Akaike Information Criterion corrected for small sample size ( $AIC_c$ ), or the adjusted  $QAIC_c$  value in cases where we observed slight overdispersion in the global model ( $c\text{-hat} > 1$ )<sup>103,105</sup>. We model-averaged the beta values of covariates appearing in all models returning a  $\Delta AIC_c$  or  $\Delta QAIC_c < 2$  (Supplemental Information, Table S3) and retained significant detection predictors for subsequent analyses<sup>105</sup>. We then generated 64 single-species, single-season occupancy (habitat use) models for each species<sup>97</sup>, holding constant the retained detection variables from above, to determine which of our six habitat use variables were important for each focal species (models listed in Supplemental Information, Table S4). As in the detection modeling, we ranked habitat use candidate models by  $AIC_c$  or  $QAIC_c$  and retained all significant habitat use predictors for use in our third step. The model averaged habitat use estimates for each species across all camera locations were calculated using the top-performing models (Supplemental Information, Table S5).

Finally, we evaluated the influence of coyotes on the habitat use probabilities of mesopredators using the detection and habitat use variables that were included in the top respective models and returned beta values with 95% confidence intervals that did not overlap 0 to formulate sets of conditional two-species occupancy models<sup>94,95</sup>. These models estimate the influence of a species assigned as 'dominant' (in our case, coyotes) on the probability of habitat use by species deemed as 'subordinate'. Within these model sets, one set for every pairwise interaction between coyotes and possible subordinates ( $N = 4$  model sets), we altered covariates in the models to allow for or disregard the ability of coyote presence to impact a subordinate's probability of habitat use or detection and



ranked each model using  $AIC_c$ . We model-averaged the use probabilities of both coyotes (Species A) and the subordinate species (Species B) from each model, returning an  $AIC_c$  score of  $< 2$  and used them for calculating Species Interaction Factors (SIFs) between each pairing of species using the equation:

$$SIF = \frac{\psi_A * \psi_{BA}}{\psi_A * (\psi_A * \psi_{BA} + (1 - \psi_A)) * \psi_B} \quad (1)$$

where  $\psi_A$  is the use probability by the dominant species A;  $\psi_{BA}$  is the use probability by the subordinate species B in the presence of species A; and  $\psi_B$  is the use probability by species B when species A is absent (Richmond 2010). Values of  $SIF > 1$  suggest that dominant (A) and subordinate (B) species are co-occurring more often than expected by chance. In contrast,  $SIF < 1$  indicates that both species co-occur less often than expected by chance.  $SIF$  values  $\sim 1$  indicate no detectable effect of Species A on the habitat use probability of Species B<sup>94,95</sup>. All statistical analyses were performed using the package RPresence<sup>106</sup> within R Statistical Software<sup>107</sup>.

## Results

### Coastal mesopredator assemblage

We conducted 75,576 camera trapping hours over 18 months, capturing  $> 1.5$  million images across 108 camera sites. We detected seven mesopredator species, including coyotes, red foxes, raccoons, feral or free-ranging cats (hereafter “cats”, *Felis catus*), striped skunks (*Mephitis mephitis*), American mink (*Neogale vison*), and Virginia opossums (hereafter “opossums”, *Delphinus virginiana*). Raccoons, red foxes, and opossums were the most frequently recorded (highest number of images) and most widespread (highest number of sites) mammalian carnivores. Coyotes and cats were comparatively less frequent and more sparsely distributed, while striped skunks and mink were even more rare and extremely localized. Raccoons occurred at 92 of 108 camera locations (85%), followed by red foxes (78%), opossums (73%), cats (35%), coyotes (33%), striped skunks (26%), and American mink (14%; Fig. 2). These percentages represent the naïve occupancy (habitat use) of mesopredator species in our study area. We removed striped skunks and American mink from further analyses due to the relatively rare and extremely localized records of both.

Across our entire study area, the mean modeled habitat use rate was highest for raccoons at 0.88 (95% CI 0.86–0.90). Red foxes and opossums both also exhibited relatively high habitat use rates across all sites: 0.83 (95% CI 0.81–0.85) and 0.77 (95% CI 0.74–0.80), respectively. Coyotes and cats returned the lowest habitat use rates at 0.56 (95% CI 0.51–0.61) and 0.40 (95% CI 0.35–0.45), respectively, (Fig. 3).

### Factors influencing habitat use of coastal mesopredators

Covariates significantly influencing species-specific detection probabilities were incorporated into the models to determine habitat use (Table 1). Opossums were easier to detect during the summer ( $\beta = 0.73$ , 95% CI 0.20–1.26), while red fox detectability declined in summer ( $\beta = -0.78$ , 95% CI  $-1.23$ – $-0.33$ ). Opossums, cats, and coyotes exhibited higher detectability at camera locations close to human development ( $\beta = -0.53$ , 95% CI  $-0.80$ – $-0.26$ ,  $\beta = -0.77$ , 95% CI  $-1.48$ – $-0.06$ , and  $\beta = -2.29$ , 95% CI  $-3.02$ – $-1.56$ , respectively). Coyote detection increased at the times of equinox, when photoperiod values were nearest to 12 h a day ( $\beta = 0.58$ , 95% CI 0.17–0.99). Finally, raccoons were better detected at locations with a higher percentage of cover in the immediate surrounding area ( $\beta = 0.43$ , 95% CI 0.16–0.70).

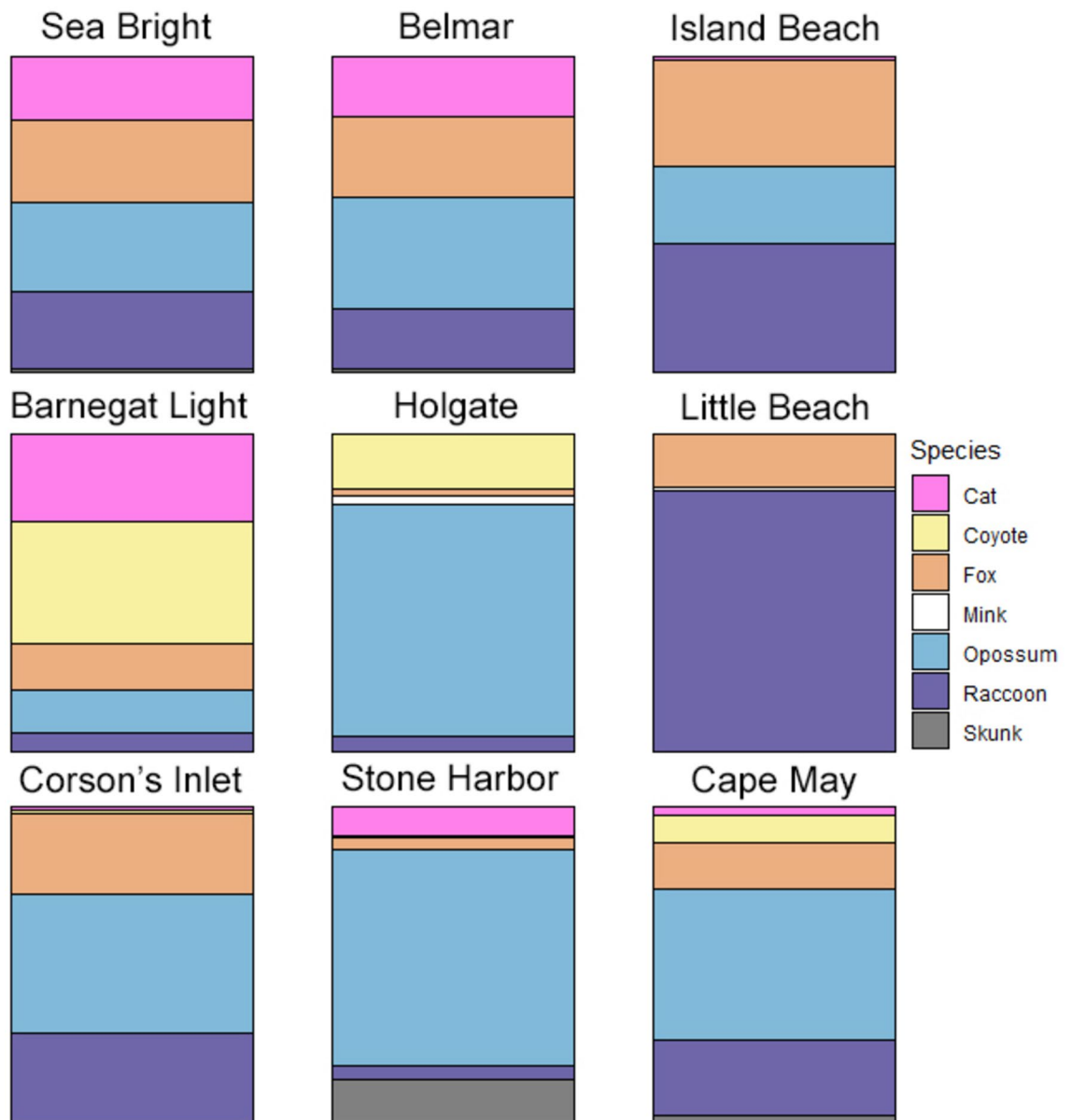
Drivers of habitat use varied significantly among species and encompassed variables ranging from prey availability, degree of landscape modification, and proximity to wetlands (Table 2). Coyotes were more likely to use areas farther from human development ( $\beta = 4.91$ , 95% CI 0.21–9.61) and close to vegetation ( $\beta = -0.86$ , 95% CI  $-1.64$ – $-0.08$ ). Raccoons were more likely to use areas closer to wetlands ( $\beta = -0.81$ , 95% CI  $-1.54$ – $-0.08$ ), while opossums were more likely to use areas with more lagomorph and rodent activity ( $\beta = 1.95$ , 95% CI 0.23–3.67). Cats were more likely to use habitats within areas of dense human populations ( $\beta = 1.10$ , 95% CI 0.18–2.02). Our models revealed no significant predictor of red fox habitat use among the variables tested (Fig. 4).

### Interaction factors of coastal predators

Sympatric coyote habitat use significantly reduced habitat use by cats, with a mean SIF value of 0.53 (95% CI 0.24–0.82; Fig. 5). Cats were absent from 70 of 108 camera locations, 29 (41%) of which were used by coyotes. Similarly, the mean SIF value for red foxes and coyotes was 0.57 (95% CI 0.35–0.79); of the 24 camera locations where we did not detect foxes, 18 (75%) had coyotes present. We found no significant relationship between coyote and raccoon habitat use [mean SIF = 0.82 (95% CI 0.62–1.02)]. Finally, none of the supported models for opossum/coyote sympatric habitat use were indicative of coyotes impacting opossum habitat use, resulting in a SIF value between coyotes and opossums of 1.00 (95% CI 1.00–1.00).

## Discussion

We found that sympatric habitat use by coastal coyotes deters habitat use by red foxes and cats, effectively defining coyotes in ocean-exposed coastal habitats as apex predators. Trophic cascade patterns within the Canidae family are well documented<sup>55,58,108,109</sup>. Within this family, many species have similar life histories and overlapping diets<sup>56</sup>, and thus are highly congruous in their resource needs<sup>110</sup>. Therefore, trophic interactions among canids are largely determined by body size and indirect interactions<sup>55</sup>. Our findings show that this pattern continues within coastal regions with coyotes and red foxes. Conversely, the impact that a coyote has on cats within our system is likely a result of both direct and indirect interactions between the two species. Though there is significant dietary overlap between coyotes and free-ranging cats<sup>29,83</sup>, wherein the larger coyote likely outcompetes cats, coyotes will also target sympatric cats in the form of both extra-predatory and predatory killings<sup>54,111</sup>. It is also

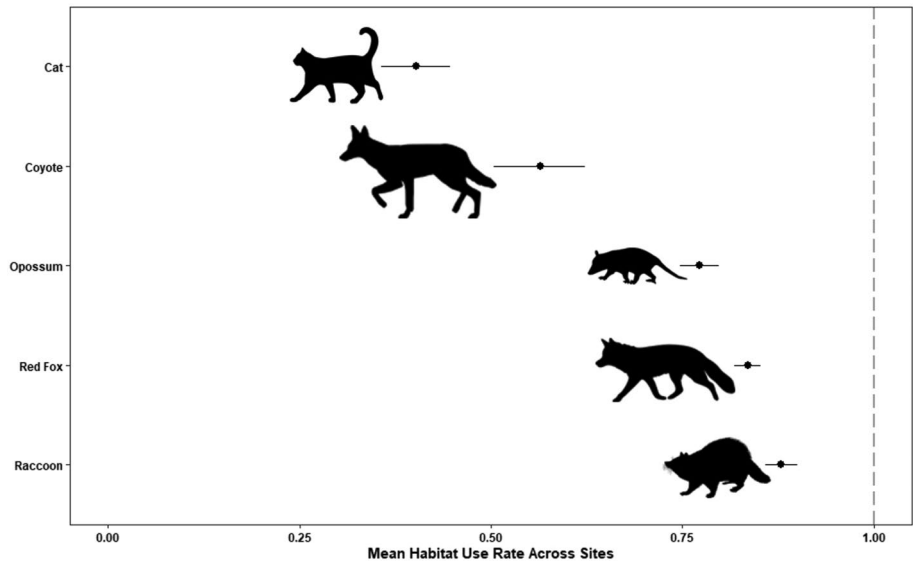


**Figure 2.** Composition of the coastal predator community detected by camera trapping in New Jersey (Localities are shown in Fig. 1) from 2019 to 2020. The size of each portion of stacked bars for each species is proportional to the percentage of images recorded for a species at a site.

possible that the diverging responses of cat and coyote use towards human modified landscapes (Fig. 4) served to further reduce their overlapping use of the same habitats.

While our findings demonstrate that coyote habitat use strongly impacted use by red foxes and cats, coyotes only slightly influenced raccoon habitat use. The mesopredator release hypothesis postulated by Crooks and Soulé<sup>27</sup> highlights that larger carnivores will have top-down impacts on smaller carnivores. While this pattern seems repeated in predator guilds consisting of species with high dietary overlap, the interaction between highly carnivorous species and omnivorous carnivores is seemingly more nuanced<sup>112</sup>. Raccoons have a broad dietary and fundamental niche and have shown a capacity to be highly successful synanthropes<sup>81,84,91,112</sup>. These traits lend to an ability to avoid competition or interaction with the larger, less synanthropic, and more carnivorous coyote through resource partitioning<sup>83,113,114</sup>. Further, raccoons do not increase their vigilance at feeding sites where coyotes are present<sup>62</sup> suggesting that coyotes do not create a landscape of fear for raccoons. Thus, the lack of significant change to raccoon use in our study area when coyotes are sympatric aligns with the established understanding of the relationship between the two species.

Habitat use by opossums was not significantly modified by coyotes; this is surprising, as coyotes are known to be major predators of opossums. One study looking at opossum mortality in the U.S. state of Kansas found that 65% of recovered opossum carcasses had been predated by coyotes<sup>115</sup>. Besides direct impacts, such as predation, there is little to no evidence within the literature of opossums being impacted by the top-down controls of apex



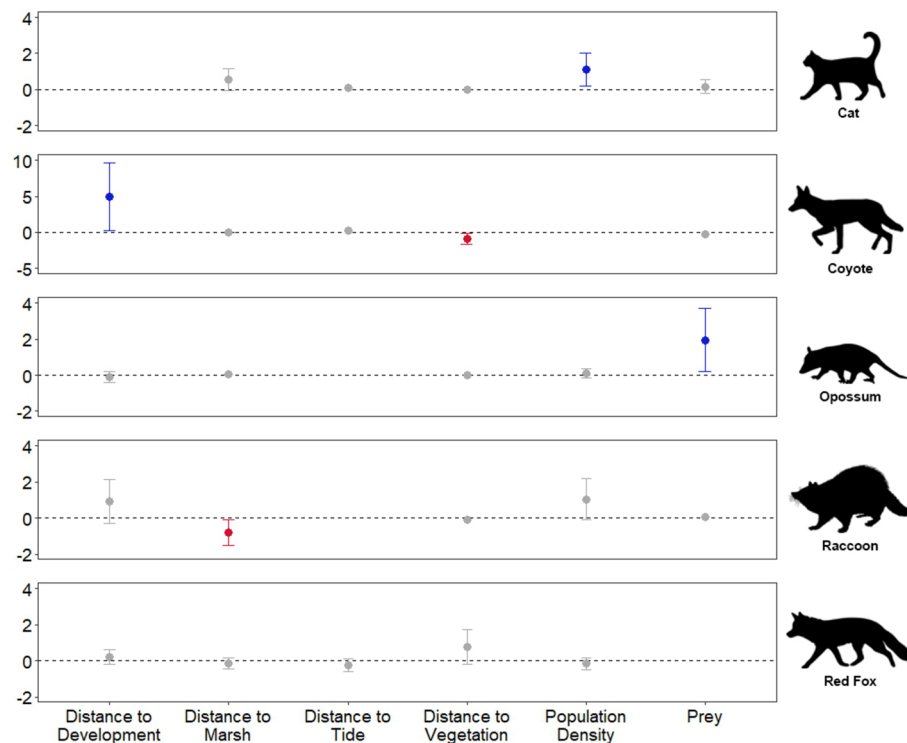
**Figure 3.** Mean habitat use rates for five focal species across all 108 camera locations from surveys conducted in 2019–2020 in coastal New Jersey, USA. Estimates are derived from the model averaged habitat use values for single-species, single-season occupancy models for each species and habitat use rates are the mean across all 108 camera locations. Error bars represent 95% confidence intervals.

Focal species	Distance to development	Distance to vegetation	Vegetation cover percent	Beach population	Photoperiod squared	Photoperiod
Cat ( <i>Felis catus</i> )	− 0.77 (± 0.71)	<b>0.46</b> (± 0.33)	− 0.02 (± 0.06)	− 0.05 (± 0.16)	0.03 (± 0.08)	0.04 (± 0.12)
Coyote ( <i>Canis latrans</i> )	− 2.29 (± 0.73)	− 0.66 (± 1.00)	− 0.30 (± 0.33)	− 0.05 (± 0.12)	<b>0.58</b> (± 0.41)	0.48 (± 1.01)
Opossum ( <i>Didelphis virginiana</i> )	− 0.53 (± 0.29)		− 0.06 (± 0.12)	<b>0.73</b> (± 0.53)	− 0.03 (± 0.08)	0.03 (± 0.08)
Raccoon ( <i>Procyon lotor</i> )	0.04 (± 0.10)	− 0.01 (± 0.04)	<b>0.43</b> (± 0.27)	− 0.04 (± 0.10)		
Red Fox ( <i>Vulpes vulpes</i> )	0.03 (± 0.08)		− 0.04 (± 0.10)	− 0.78 (± 0.45)		

**Table 1.** Parameter estimates (with 95% CIs) for model averaged detection probabilities of focal species. Bold values have 95% confidence intervals that do not overlap 0. Missing values indicate a parameter’s lack of inclusion in the top performing models for that focal species’ detection.

Focal species	Distance to development	Distance to vegetation	Distance to high tide line	Distance to wetland	Prey activity	Human population density (1 km <sup>2</sup> )
Cat ( <i>Felis catus</i> )		− 0.02 (± 0.08)	0.08 (± 0.20)	0.55 (± 0.51)	0.17 (± 0.35)	<b>1.10</b> (± 0.92)
Coyote ( <i>Canis latrans</i> )	<b>4.91</b> (± 4.70)	− 0.86 (± 0.78)	0.22 (± 0.33)	0.02 (± 0.06)	− 0.21 (± 0.43)	
Opossum ( <i>Didelphis virginiana</i> )	− 0.12 (± 0.25)	0.01 (± 0.04)		0.04 (± 0.10)	<b>1.95</b> (± 1.74)	0.12 (± 0.26)
Raccoon ( <i>Procyon lotor</i> )	0.92 (± 1.22)	− 0.08 (± 0.18)		− 0.81 (± 0.73)	0.05 (± 0.20)	1.03 (± 1.14)
Red Fox ( <i>Vulpes vulpes</i> )	− 0.21 (± 0.41)	0.77 (± 0.96)	− 0.24 (± 0.33)	− 0.15 (± 0.27)		− 0.17 (± 0.35)

**Table 2.** Parameter estimates (with 95% C.I.s) for model averaged habitat use of focal species. Bold values have 95% confidence intervals that do not overlap 0. Missing values indicate a parameter’s lack of inclusion in the top performing models for that focal species’s habitat use.



**Figure 4.** Beta coefficients from site occupancy models for predictors of habitat use by coastal predators in New Jersey, USA for predators captured in 2019–2020. Error bars are 95% confidence intervals. Grey dots indicate a beta coefficient value with confidence intervals that overlaps 0. Blue (positive) and red (negative) dots indicate a beta coefficient value with confidence intervals that do not overlap 0 and is thus considered significant.

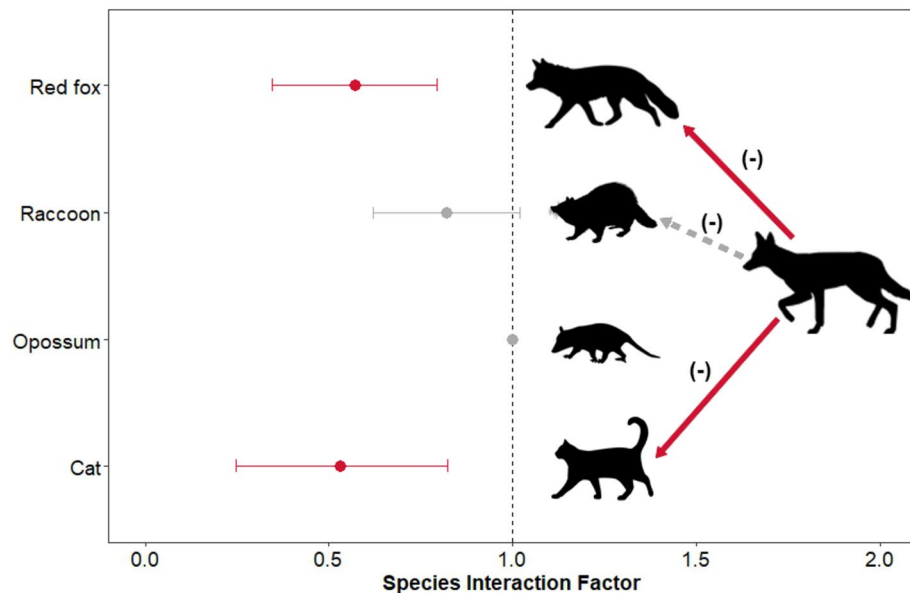
predators, likely due to their wide fundamental niche<sup>63,116</sup>. Similar to raccoons, opossums have an extremely wide dietary niche<sup>85,116</sup>, which would lessen any direct competition over food resources. Opossums are also extremely synanthropic<sup>117</sup> and can access resources that may be unavailable to coyotes, further easing any niche overlap and reducing competition<sup>118</sup>.

None of the habitat preferences exhibited by the species within our study overlapped. In fact, cats and coyotes showed opposing reactions to humans. Cats exhibited higher use of camera locations with a higher human population density, likely due to their high reliance on human subsidies<sup>48,119</sup>. Meanwhile, during the coyote expansion across North America, their preference for pockets of natural refugia in otherwise urban areas has been well documented<sup>50,58,59</sup>. Along the highly developed New Jersey coastline, coyotes select natural habitat remnants in state and federal parks and preserves (> 90% of coyote detections occurred within Barnegat Light State Park, Cape May Point State Park, and the Holgate Unit of the Edwin B. Forsythe National Wildlife Refuge), especially areas with more vegetative cover (Fig. 4). Raccoons exhibited no significant relationships with human development or population density, suggesting that environmental conditions primarily drive their habitat use. For example, raccoons in our study used areas that were close to, or within, wetlands, which are often used disproportionately more than other habitat, when available<sup>120</sup>. In coastal areas, raccoon diets commonly include mollusks, crabs, and other marine or freshwater invertebrates and fish<sup>84,121,122</sup>. Further, though wetland areas are prone to flooding, especially in coastal regions where tidal levels frequently change<sup>38,43</sup>, the arboreal attributes of raccoons allow for their persistence through these sporadic high water levels<sup>123</sup>.

Like raccoons, opossums showed no significant relationship to human development or population density. The only correlation for their use was that opossums used habitats with high numbers of rodents and lagomorphs. Though opossums are functionally capable of predation, their diet relies heavily on carrion, insects, and plant material<sup>85,116</sup>. We, therefore, attribute this correlation to the similarities between opossum ecology and that of the rodent and lagomorph species we documented. Rodent (carrion and plant material<sup>124</sup>) and lagomorph (plant material<sup>125</sup>) diets are similar to opossums, indicating a likely overlap in habitat preferences. Further, all three taxa are highly synanthropic<sup>126</sup>, allowing them to capitalize on anthropogenic subsidies and coexist in urban habitats.

Red foxes exhibited no preference for any of our tested habitat features (Fig. 4). Red foxes are one of the most highly adaptable mammals and have shown an ability to thrive in many habitat types<sup>69</sup>. Similar to raccoons and opossums, the catholic diet of red foxes<sup>127</sup> allow for their remarkably broad and diverse habitat distribution<sup>110</sup>. In fact, red foxes often select areas with a high interspersed of diverse microhabitats<sup>128–130</sup>. Within our study, red foxes were ubiquitous (Fig. 2) and frequent visitors to most camera locations. Notwithstanding the broad suite of environmental conditions that red foxes can successfully exploit, there was one factor that significantly determined their spatial pattern of occurrence: the presence of the largest carnivore in the food web—coyotes.





**Figure 5.** Mean modeled species interaction factors (SIFs) for coyotes when paired with the four other focal species (cat, opossum, raccoon, and red fox) in coastal New Jersey, USA from 2019 to 2020. Error bars are 95% confidence intervals of the mean SIF value from calculated from the mean of all 108 camera location SIFs and the mean SIF value's distance from 1 directly correlates to the strength of the change in estimated use probability due to the presence of coyotes. Red dots represent values that do not have their 95% confidence interval overlapping 0 and are thus considered significant. Any values below 1 indicate that the two species are interacting less than expected by chance, an indicator of avoidance of the dominant species by the subordinate species. SIF values of 1.0 indicate no impact of coyote presence on subordinate species' use probabilities. Opossum SIF lacks error bars due to all supported opossum-coyote interaction models lacking an impact of coyote occurrences upon opossum use probabilities, resulting in a mean SIF value of  $1.0 \pm 0.0$  between the species.

The east coast of North America is one of the most recent areas of the geographic expansion of coyotes<sup>50</sup>. The low levels of coyote use in our study area, shown by their relatively low mean habitat use rate across our sites (Fig. 3), is likely an indication of an ongoing colonization process within the region. As coyotes are highly fecund (e.g. ~7 pups per litter when population densities are low<sup>131</sup>) and can quickly expand over large geographic areas<sup>50</sup>, their densities in coastal regions will likely increase rapidly in the near future. Though our study shows that coyotes avoid areas under anthropogenic influence, coyotes elsewhere have had success in areas of dense human population (i.e. Chicago, U.S.<sup>132</sup>, New York City, U.S.<sup>59</sup>, Southern California<sup>133</sup>). We suspect that increasing coyote density will drive subordinate individuals towards areas closer to human development.

Currently, though relatively rare, coyotes are sympatric with all four of our other focal species (Fig. 2) and potentially impart top-down controls on at least red foxes and cats. All our non-coyote focal species are considered supreme synanthropes<sup>126</sup>, and as such will likely avoid any top-down impacts of coyotes by utilizing more resources available in the areas near to urban development, an example of the 'human-shield hypothesis'<sup>61,118</sup>. As the coyote densities increase along the coast, their effectiveness as apex predators exhibiting top-down controls may be habitat driven. In areas near to human subsidy, where food resources are abundant and constant, competition will likely be eased, and coyotes may represent just another member of a dense, anthropogenically reliant mesopredator guild. In areas farther from human disturbance and subsidy, the size and aggression of coyotes will likely reduce spatial and temporal overlap of at least red foxes and cats, and possibly raccoons with sympatric coyotes.

The dual role of coyotes as apex and mesopredator suggests that the effects of coyotes, in the context of conserving threatened prey species, will vary along a spectrum of population density and habitat type. In areas of low resource availability far from human subsidy, their ability to competitively exclude or kill other predators will likely reduce overall predation pressure for threatened species that are endemic to coasts. Coyotes inhabiting coastal dunes and traversing the strandlines of ocean beaches may deter red foxes and cats from targeting prey species of conservation concern (e.g., beach-nesting birds)<sup>134,135</sup>. Conversely, in areas of higher resource availability synanthropic coyotes will likely impose additive predation pressure on species already stressed by multiple synanthropic mesopredators [e.g. coyotes may target colonies of nesting shorebirds<sup>37</sup>]. Understanding how the trophic dynamics of increasing coyote populations in coastal food webs will evolve over time is clearly a research priority in a conservation context. At present, allowing for coyote persistence to control smaller carnivores that threaten birds and reptiles breeding in coastal areas has potential, especially in areas lacking human subsidy where our results indicate coyotes are presently more prevalent. However, details about the exact trophic role of coyotes in these habitats (e.g., predatory impact on already threatened populations) and their wider effects on

species distribution warrant further clarification. Nevertheless, the fact that novel apex predators can become established in coastal food webs illustrates the highly dynamic nature of conservation challenges for habitats and species at the edge of the sea.

## Data availability

Data are available from the corresponding author, Christian Crosby, by request.

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## Author contributions

B.M. and T.S. conceived the study. C.C., B.M., and K.K. performed the data collection. C.C. performed the data analysis. C.C., B.M., and T.S. discussed the results and drafted the manuscript. All authors provided comments on the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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