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Invasive plant *Arundo donax* alters habitat use by carnivores

Molly Hardesty-Moore ⓘ · Devyn Orr · Douglas J. McCauley ⓘ

Abstract Invasive plants can have significant negative interactions with native flora and fauna, often decreasing the abundance and diversity of native plants and invertebrate and vertebrate herbivores. Less is known, however, about how invasive plants influence higher-order consumers, such as carnivores. *Arundo donax* is a globally distributed invasive grass that forms dense monotypic stands in the habitats where it successfully establishes. This study investigated the influence of *Arundo* invasion on mammal assemblages in California's Santa Clara River Valley. Specifically, we aimed to determine whether *Arundo* alters habitat use for carnivores, and if so, assess the possible mechanisms driving these differences. We used remote cameras to evaluate carnivore habitat use and model occupancy, and live traps and remote cameras to assay abundance of small mammals, common prey of these larger predators. We found that detections of all carnivores were significantly lower in *Arundo*-dominated habitat patches, suggesting decreased preference for *Arundo* habitat. This was reflected in the occupancy model, which found the highest probability of coyote and bobcat habitat use in native patches and lowest in *Arundo*; however, habitat did not seem to be as important of a predictor as in the pooled species results. Small mammal abundance was similar if not higher in *Arundo*, suggesting the possibility of *Arundo* acting as a refuge for prey species and altered predator–prey dynamics in *Arundo*-dominated patches. This study improves our knowledge of the often-complex ways that invasive plants, like *Arundo*, influence the ecology and behavior of faunal communities in invaded ecosystems.

Keywords *Arundo donax* · Invasive plant · Mammal · Riparian · Occupancy · Carnivore

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Introduction

Invasive plant species have substantial and long-lasting effects on local ecosystems by decreasing abundance and diversity of native species, disrupting ecosystem processes such as nutrient cycling and fire regimes, and altering species interactions and food web structure (Brooks et al. 2004; Vilà et al. 2011; Smith-Ramesh 2017). While we are beginning to

understand the effects of invasive plants on native plants, arthropods, birds, pollinators, and soil communities (Vilà et al. 2011), little is yet known about the ways by which invasive plants directly or indirectly alter mammal assemblages, particularly mammalian carnivores and omnivores—despite the abundance of mammals in many invaded regions and their vulnerability to habitat loss and alteration.

If plant invasions negatively influence mammalian carnivores, the ecological repercussions could be significant. Other anthropogenic impacts on carnivores, such as habitat fragmentation (Crooks et al. 2017), have, for example, dramatically altered ecological function via pathways such as trophic cascades (Schmitz et al. 2000, Ripple and Beschta 2012). Carnivores, while at times in conflict with humans, also provide ecosystem services (O'Bryan et al. 2018); for example, red foxes (*Vulpes vulpes*) can potentially regulate Lyme disease through predation on mice (Levi et al. 2012), and recolonization of mountain lions (*Puma concolor*) can reduce deer density and decrease risk of human mortality from deer-vehicle collisions (Gilbert et al. 2017).

Plant invasions have altered riparian watersheds globally, endangering these sensitive and biodiverse ecosystems (Lambert et al. 2010), which are often important habitat for carnivores and other mammals. Riparian watersheds have high resource availability (e.g. water, food, shelter; Hilty and Merenlender 2004), and in an agricultural-urban landscape, riparian zones can provide one of the few remaining connectivity pathways for far-ranging carnivores between otherwise-fragmented landscapes (Naiman et al. 1993; Gillies and Clair 2008).

Invasive plants can alter these riparian ecosystems by changing the physical structure of habitats and landscapes and reducing the availability of food resources. For instance, invasive plants such as *Tamarix* spp. and honeysuckle (*Lonicera maackii*) can provide dense vegetated understory that change the way small and medium mammals use habitat (Dutra et al. 2011; Bateman and Ostoja 2012), and many invasive plants monopolize habitat, increasing vegetation density and decreasing diversity of food resources available to invertebrate and vertebrate herbivores and omnivores (Bell 1997; Brooks et al. 2004), thus potentially decreasing food availability to carnivores as well.

In southern California, riparian habitats are extremely endangered, with only an estimated 5% remaining with relatively natural biological and physical structure (Katibah 1984; Bell 1997). One of the greatest threats to remaining southern California riparian ecosystems is the invasive plant *Arundo donax*, a perennial reed-like grass, which has invaded subtropical and warm temperate regions globally—including Africa, Australia, Europe and the Americas (Bell 1997; Giessow et al. 2011; U.S. Fish and Wildlife Service 2017). *Arundo* is a large-statured invasive grass, a life form of invasive plant predicted to have strong interactions in invaded ecosystems (Lambert et al. 2010). Like other large-statured invasive grasses (e.g. *Phragmites australis*), *Arundo* is an aggressive competitor, outcompeting native plants through massive clonal growth. *Arundo* can alter flow regimes, increase risk of fire, and form monotypic habitat (Bell 1997; Herrera and Dudley 2003). *Arundo* also decreases diversity and abundance of animal species, including native arthropods, birds, and bats (Herrera and Dudley 2003, Kisner 2004, Orr et al. in review). This diversity of ecosystem and community effects driven by *Arundo* invasion would seem likely to have an impact on carnivores as well.

We propose two potential mechanisms that could alter carnivore use of habitat in *Arundo* patches. First, lower plant diversity, habitat heterogeneity, and the low palatability of *Arundo* (Bell 1997) could decrease the presence of smaller vertebrate herbivores, thereby limiting food available for carnivores (i.e. limited prey mechanism). Evidence from previous studies on birds and arthropods, potential prey species of carnivores, suggests some support for this mechanism (Herrera and Dudley 2003, Kisner 2004, Orr et al. in review). Second, the high density of *Arundo* could increase the energetic cost of movement in these patches, decreasing or blocking the ability of larger-bodied species to travel through *Arundo* (i.e. limited movement mechanism). Additionally, this mechanism incorporates a decreased ability to hunt in dense *Arundo* patches, especially for coursing predators (e.g. coyotes). We note, however, that the *Arundo* patches could have a variable influence on carnivores, as the dense vegetation could provide cover for ambush predators, such as bobcats.

Here, we aim to determine whether *Arundo* alters carnivore habitat use in a riparian corridor in southern California and test the proposed mechanisms listed

above. Under the limited prey mechanism, we would expect to find lower prey density and also fewer carnivores; whereas, under the limited movement mechanism, we would expect to see fewer carnivores but not necessarily lower prey density, perhaps even elevated levels of prey due to a predator refuge effect (Dutra et al. 2011). We could also expect to see differential effects across carnivores under the limited movement mechanism based on body size (i.e. larger species could face greater energetic costs) and hunting mode (i.e. ambush predators could benefit from dense vegetation, whereas coursing predators could be at a disadvantage). We test these against the null hypothesis that *Arundo* does not have an effect on carnivores.

Methods

Study site

We conducted this study along the Santa Clara River (SCR), which spans 134 km from the Transverse Ranges to its mouth near Ventura, California. The SCR has highly variable annual stream flow, which depends on the intensity of rainfall each year. During the wet season of 2017 and 2018, there was a high level of precipitation that caused the river to flood (542 mm in winter 2017 and 279 mm in winter 2018; VCWPD 2019). During the dry season, water flow is substantially reduced, leaving dry riverbed in some regions (Warrick et al. 2005). The study area encompasses a 27 km stretch of the SCR, between the cities of Ventura and 7 km northeast of Santa Paula (Fig. 1a). This section of the SCR is surrounded on either side by agricultural fields and orchards (e.g. kale, oranges, rosemary, etc.) and urban development, making the riparian zone some of the only relatively undeveloped habitat in the valley. Vegetation, other than *Arundo*, consists primarily of willows (*Salix exigua, S. lucida, S. laevigata, S. lasiolepis*), cottonwood (*Populus fremontii, P. trichocarpa*), coyote brush (*Baccharis pilularis*), and mulefat (*B. salicifolia*) (Bell 1997; Going and Dudley 2008).

Land cover classification

The Nature Conservancy and Stillwater Sciences initially classified land cover using satellite imagery and ArcGIS (v. 10.2, Overlay toolset). *Arundo* was visually classified in Google Earth (Google Earth, 2015) along the SCR and estimated percent cover estimates were assigned within habitat patch polygons in ArcGIS (Stillwater Sciences and California State Coastal Conservancy 2015). Using this landscape classification and our own ground-truthing, we delineated three habitat categories: native (< 30% *Arundo*), mixed (30–70% *Arundo*) and *Arundo* (> 70% *Arundo*) (Fig. 1). Based on the three categories, we scouted potential habitat patches and verified the habitat type visually using estimates of percent *Arundo* cover. Habitat patches were chosen for use in this study based on size (> 1.5 ha), location (> 200 m from patch of same habitat type), and accessibility (available access roads or trails).

Remote camera methods

We deployed remote-activated cameras at three sites along the SCR (Fig. 1a), primarily on The Nature Conservancy property. Within the three sites, we selected two patches of each of the three focal habitat types (native, mixed, and *Arundo*; Fig. 1b) and placed one Bushnell Essential E2 camera in each, for a total of six cameras per site and 18 cameras overall (2917 trap nights). Habitat patches within a site were at least 200 m from a patch of the same habitat type, and each site was at least 3.5 km from another site. We placed cameras at least 50 m from the patch edge for native and mixed, and at least 20 m from the patch edge for *Arundo* due to density of vegetation and relatively smaller patch sizes. The final camera location was chosen based on haphazardly selected GPS locations. We placed cameras on trees when available, and sturdy brush or clump of *Arundo* otherwise, 0.5–1 m from the ground. We monitored the cameras for 3 months at a time. There were three sampling sessions that spanned wet and dry seasons: August–November 2016 (dry season), March–June 2017 (wet season), and March–June 2018 (wet season). Wet season sampling periods were timed such that the cameras were deployed after peak rainfall to capture the period with strong river flow and avoid major flooding events.

Small mammal trapping

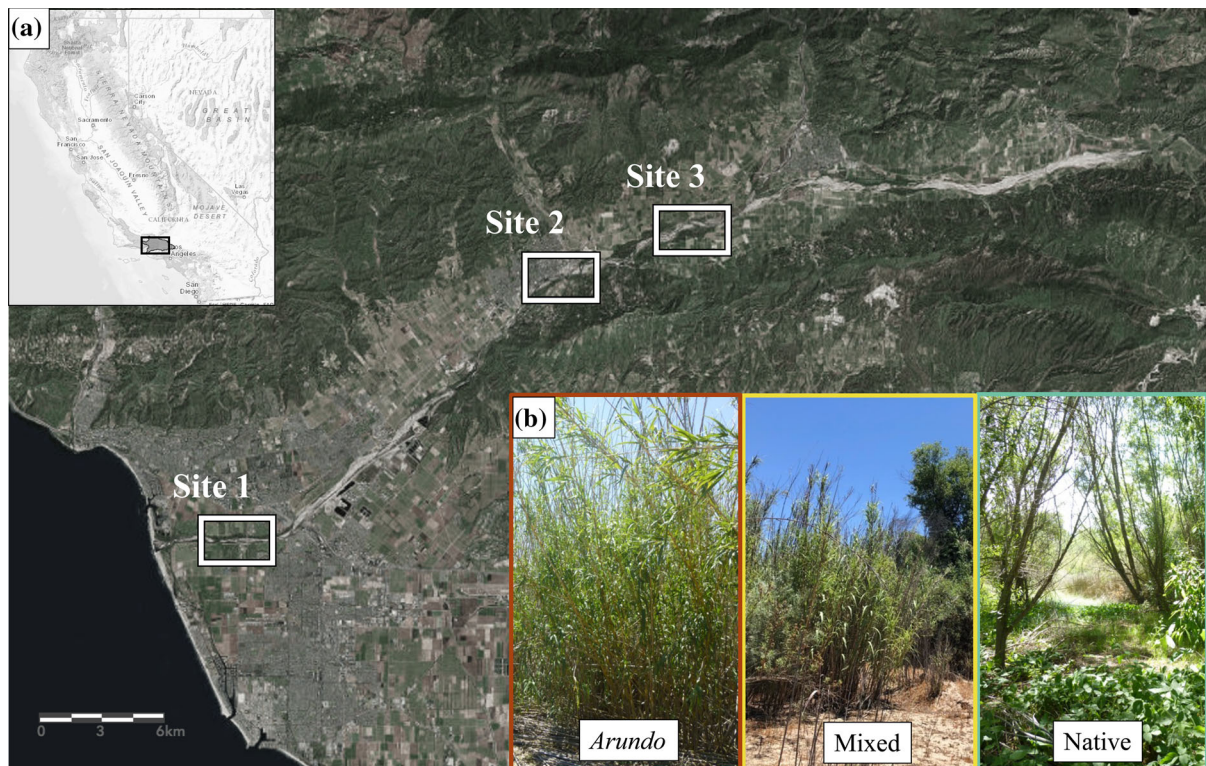We live-trapped small mammals in November 2017 and June 2018 at Site 3. We chose this site because it

Fig. 1 a Map of the three study sites along the Santa Clara River in Ventura County, California. **b** Examples of the three habitat types based on percent cover of *Arundo donax* in the habitat patch. From left to right: *Arundo* (> 70% *Arundo*), mixed (30–70% *Arundo*), native (< 30% *Arundo*). Colored outlines correspond to habitat colors represented in subsequent figures

had high consistency in camera data collection, accessibility, and permissions for live trapping. We set one trapline of thirty-eight Sherman live traps along a transect in each habitat type (native, mixed, and *Arundo*). The traps were deployed for three nights in fall 2017 and summer 2018, amounting to 684 trap nights in total.

We identified captured small mammals to species, sexed, weighed, measured, and marked with a numbered ear tag (National Band and Tag) before they were released. We recorded recaptures as well on subsequent nights. All work is authorized and described under our UCSB Institutional Animal Care and Use Committee protocol and California Department of Fish and Wildlife Scientific Collecting Permit.

Carnivore use of habitat

We estimated carnivore use of habitat using observations from camera sightings. We recorded observations of an organism a maximum of once per minute for all mammals, including prey species (rabbits, woodrats, small rodents, and ground squirrels). We then standardized detections by photographic rate—total observations divided by the number of nights the cameras were active in each habitat type during each season (Rovero and Marshall 2009; O'Brien 2011).

We applied a negative binomial generalized linear mixed model (GLMM) in R (package lme4; Bates et al. 2015) to compare detections per unit effort between habitat types, with count as the dependent variable (standardized as above); habitat, season, and the interaction of habitat by season as the potential covariates (Bateman and Ostoja 2012); and site as a random effect. We generated a marginal and conditional R^2 value for each GLMM model using R package MuMIn (Nakagawa et al. 2017; Barton 2019). We based model selection on AIC value, with the top

models defined as those with the lowest AIC and dAIC (difference in AIC values) less than two.

Occupancy model

We used an occupancy modeling approach, as described in MacKenzie et al. (2017), to estimate probability of habitat use across the three habitat types and three seasons. Due to the wide-ranging nature of these species, multiple cameras could be within an individual's home range, thus we are interpreting the occupancy results as probability of habitat use, rather than true occupancy (Tobler et al. 2015). We analyzed use patterns for two carnivores of conservation interest in the area – coyotes (*Canis latrans*) and bobcats (*Lynx rufus*)—which had temporally consistent data to build detection histories (i.e. detections across all sites and sampling periods). While Virginia opossums (*Didelphis virginiana*) and striped skunks (*Mephitis mephitis*) had numerically more detections overall, they both had five or fewer detections in each site in 2016, with no sightings of opossums in Site 3 for 2016 and 2017. The majority of the detections for these species occurred in 2018, which accounts their high overall number of detections. Thus, we chose bobcats and coyotes as our focal species to create a robust model across all three sites and sampling periods.

We applied a multi-season occupancy model using the package "unmarked" in R (Ahumada et al. 2011; Fiske and Chandler 2011; Kéry and Chandler 2016) to detection histories created using observations from the remote cameras, with fall of 2016, spring of 2017, and spring of 2018 defined as the three primary sampling periods in the model. As the cameras record continuously during a sampling period, we followed precedent and denoted each trap day (midnight to midnight) as an repeat "survey" (or secondary sampling period) at each camera station in the detection history (Tobler et al. 2015; Rich et al. 2017). We first tested for differing detection probability (p, the probability of detecting a species if it is present) by holding occupancy probability (ψ) constant (as in Negrões et al. 2010; Nogeire et al. 2013). We expected the detection rate could differ by habitat (native, mixed, and *Arundo* habitat vary in terms of visibility) or by the day of the year, and thus included habitat and Julian date as the two covariates, with year as a random effect. We then selected the best detection model or models (determined using AIC) to test for occupancy

probability, with the three habitat types as the covariate and date and year as random effects in the model. When two or more models had dAIC < 2, we assumed all could be considered "best" and used a model average to compute estimates (Burnham and Anderson 2002).

To examine if there were any differences by year that could not be captured by the multi-season occupancy model, we ran separate single-season occupancy models for both species and each year (2016, 2017, 2018).

Finally, we tested goodness of fit of the occupancy models using a χ-square method as described in the "unmarked" package (Fiske and Chandler 2019).

Small mammal prey abundance

We estimated small mammal abundance for each habitat type and sampling period using both the camera data, in which we can primarily identify larger small mammals (e.g. rabbits and squirrels), and live-trap data, which can be used to estimate abundance of smaller rodents. Methods for analyzing small mammal use of habitat from the camera data were the same as for carnivores (see "*Carnivore use of habitat*" section).

To estimate abundance using the live-trap mark-recapture data, we used Rcapture in program R (version 3.5.1). Rcapture uses the capture histories to compare models of estimated abundance, including a null model (M0), a model with variation based on time (Mt), a model with variation based on behavior (Mb), and a model with variation based on heterogeneity (Mh), which are ranked based on their AIC (Rivest and Baillargeon 2007). We chose best estimate models for each habitat type based on their AIC score. To test for differences in abundance in the live-trap data, we calculated the 95% confidence intervals based on the given standard error, then ran two-sample t-tests on habitat type to determine a *p* value.

Results

Carnivore use of habitat

Eight species of carnivores were detected by our cameras: coyotes (*C. latrans*), bobcats (*L. rufus*), striped skunks (*M. mephitis*), Virginia opossums (*D.*

virginiana), raccoons (*Procyon lotor*), long-tailed weasels (*Mustela frenata*), gray foxes (*Urocyon cinereoargenteus*), and mountain lions (*Puma concolor*) (Table 1). Coyotes were by far the most commonly detected carnivore, followed by striped skunks, Virginia opossums, and bobcats.

With all carnivore species pooled, there were more detections overall in native habitat than in mixed or *Arundo;* this pattern was consistent across all seasons

(Fig. 2). The best generalized linear mixed model for pooled carnivores included only habitat as a covariate (Table 2), although the model with habitat and season had dAIC < 2 and thus is also considered a top model. There was a significant difference between habitat types (Table S1 in Electronic Supplemental Material; $p < 0.01$), and Tukey posthoc pairwise comparison of habitat types revealed a significant difference between

Table 1 List of species detected by remote cameras in this study: the category as to whether they were included in the carnivore (denoted as "predator") analysis or small mammal (denoted as "prey") analysis; scientific name; common name; and the total number of detections of each species over all seasons, sites, and habitat types

| Category	Scientific name	Common name	Total detections
Predator	*Canis latrans*	Coyote	338
Predator	*Mephitis mephitis*	Striped skunk	140
Predator	*Didelphis virginiana*	Virginia opossum	122
Predator	*Lynx rufus*	Bobcat	112
Predator	*Procyon lotor*	Raccoon	50
Predator	*Urocyon cinereoargenteus*	Gray fox	8
Predator	*Mustela frenata*	Long-tailed weasel	7
Predator	*Puma concolor*	Mountain lion	2
Prey	*Sylvilagus* spp.	Brush rabbit, etc.	11038
Prey	Other rodent spp.	Woodrat, etc.	2576
Prey	*Otospermophilus beecheyi*	California ground squirrel	384
Prey	*Sciurus niger*	Fox squirrel	44
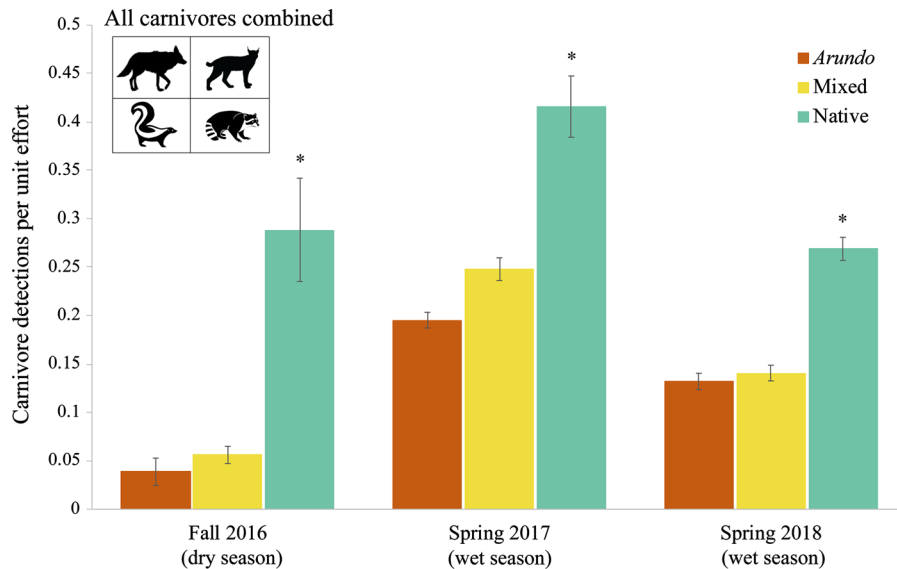
Fig. 2 Detections of carnivores standardized by unit effort (camera trap nights) in the Santa Clara River across all sampling periods. Habitat type is denoted by color: *Arundo* (orange), mixed (yellow), native (blue-green). Error bars represent standard error. There was a significant difference ($\alpha = 0.05$) in carnivore detections per unit effort between native habitat and mixed and *Arundo* habitat for all sampling periods, as indicated by the asterisks (*)

Table 2 Summary of carnivore results (all species pooled) from generalized linear mixed models showing best model fit using AIC

Explanatory variables	AIC	dAIC	Df residuals	Log-likelihood	Marginal R^2	Conditional R^2
Habitat	846.1	0	211	− 418.0	0.135	0.135
Habitat + season	847.7	1.6	210	− 417.9	0.131	0.131
Habitat * season	849.9	3.8	208	− 416.9	0.148	0.148
Season	854.9	8.8	212	− 423.4	0.015	0.043

The columns represent AIC, difference in AIC between the model and the best model (dAIC), the degrees of freedom of the residuals, log-likelihood, and marginal and conditional R^2 values. The two top models (dAIC < 2) were the habitat and habitat + season models

Table 3 Top ranked models for probability of detection (p) and occupancy (ψ) for coyotes based on the multi-season occupancy model

Model	K	AIC	dAIC	AICwt	χ^2 Goodness of fit (p value)	Probability of habitat use (SE)	Probability of detection (SE)
Detection (p) ∼							
Habitat + date	6	1406.36	0	1.000	0.17		0.088 (0.010)
Date	5	1419.03	12.68	0.002	0.12		0.094 (0.009)
Habitat	5	1445.24	38.88	3.6E−09	0.49		0.087 (0.009)
Intercept only	4	1456.03	49.67	1.6E−11	0.44		0.092 (0.006)
Occupancy (ψ) ∼							
Intercept only	6	1406.36	0	0.64	0.16	0.705 (0.123)	0.088 (0.010)
Habitat (native)	7	1407.47	1.12	0.36	0.22	0.817 (0.145)	0.088 (0.010)
Habitat (mixed)						0.701 (0.123)	
Habitat (*Arundo*)						0.551 (0.215)	
Model average (habitat and null)						0.699 (0.146)	0.088 (0.010)

K is the number of parameters in the model, dAIC is the difference between the AIC of the model and the model with the lowest AIC, and AICwt is the weight of each AIC value. The χ^2 goodness of fit p values are listed, with $p > 0.05$ indicating good model fit

native detections and mixed and *Arundo*, but no difference between mixed and *Arundo* (Table S2).

Occupancy model

The multi-season occupancy model for coyotes found both the null model and the model with habitat as a covariate to be the top models for predicting probability of habitat use (dAIC = 1.12; Table 3). The model average of the two models found probability of habitat use $\psi = 0.699$ (SE = 0.146). The null model had higher support (64%), but the habitat model had 36% support, indicating habitat type might have had some influence on probability of habitat use for coyotes. Though the habitat model had less support, there was a difference between predicted habitat use for native, mixed, and *Arundo*. Native habitat had the highest probability of habitat use for coyotes ($\psi = 0.817$, SE = 0.145) and *Arundo* had the lowest ($\psi = 0.551$, SE = 0.215). The best model for detection probability (p) of coyotes was the model with habitat and date (Table 3).

Similarly, for bobcats both the null model and the habitat model were found to be top models (dAIC = 1.66; Table 4). The model average probability of habitat use for bobcats was $\psi = 0.463$ (SE = 0.137). Though once again the null model had greater support (70%), the habitat model had 30% support, which

Table 4 Top ranked models for probability of detection (p) and occupancy (ψ) for bobcats based on the multi-season occupancy model

Model	K	AIC	dAIC	AICwt	χ^2 Goodness of fit (*p* value)	Probability of habitat use (SE)	Probability of detection (SE)
Detection (p) ~							
Habitat + date	6	735.02	0	0.550	0.05		0.051 (0.009)
Date	5	735.45	0.43	0.450	0.04		0.050 (0.007)
Habitat	5	757.59	22.57	6.9E−06	0.00		0.049 (0.007)
Intercept only	4	758.91	23.88	3.6E−06	0.02		0.048 (0.005)
Occupancy (ψ) ~							
Intercept only	6	735.02	0	0.70	0.01	0.463 (0.121)	0.051 (0.009)
Habitat (native)	7	736.68	1.66	0.30	0.06	0.549 (0.189)	0.051 (0.009)
Habitat (mixed)						0.462 (0.122)	
Habitat (*Arundo*)						0.378 (0.182)	
Model average (Habitat and null)						0.463 (0.137)	0.051 (0.009)

K is the number of parameters in the model, dAIC is the difference between the AIC of the model and the model with the lowest AIC, and AICwt is the weight of each AIC value. The χ^2 goodness of fit *p* values are listed, with $p > 0.05$ indicating good model fit

could indicate some signal of habitat type in predicting habitat use. Probability of bobcat habitat use in native was highest (ψ = 0.549, SE = 0.189) and *Arundo* was lowest (ψ = 0.378, SE = 0.182). The best model for detection probability of bobcats was the model with habitat and date as well.

The multi-season occupancy models accounted for variance between the three sampling periods and examined large-scale patterns but did not provide information on how patterns may have changed between the years. The single-season occupancy models revealed that although bobcats followed the overall pattern of the habitat and null models being similar (Tables S6-S8), there was one year (2017) for coyotes when the habitat model emerged as the best (dAIC > 4; Table S4). The predicted habitat use for coyotes varied greatly by habitat type for 2017, with native ψ = 0.961 (SE = 0.057), mixed ψ = 0.764 (SE = 0.138), and *Arundo* ψ = 0.296 (SE = 0.178). The other 2 years (2016 and 2018) did not show a significant difference between the habitat and null models for coyotes (Tables S3 and S5).

Small mammals

Three small mammal prey species were detected by the cameras, brush rabbits (*Sylvilagus bachmani*), California ground squirrels (*Otospermophilus bee-cheyi*), and fox squirrels (*Sciurus niger*), along with various small rodents (Table 1). The most commonly detected small mammal prey species by the cameras were rabbits (primarily *S. bachmani*), followed by rodents, predominantly woodrats (*Neotoma* sp.). The best generalized linear mixed model of small mammal detections included only season as an explanatory variable; including habitat did not improve the model (dAIC > 2; Table S9). This indicated the type of habitat was not the most important variable for explaining small mammal detections in the camera data, although the models with habitat and habitat and season had dAIC < 4, which could indicate marginal importance. There was no significant difference in small mammal detections between the fall and spring sampling seasons (Tables S10 and S11).

Two species of small rodent were primarily caught during the live trapping: *Peromyscus maniculatus* and *P. boylii*. Small mammal abundance was estimated using the mark-recapture live-trap data from Site 3 in Fall 2017 and Spring 2018 (Fig. 3; Table S12). The estimate for small mammal abundance in 2017 was highest in *Arundo* (37.2, SE = 5.8), and in 2018 estimated abundance was highest in mixed habitat (53.3, SE = 9.1). Native habitat consistently had the lowest estimated abundance of small mammals
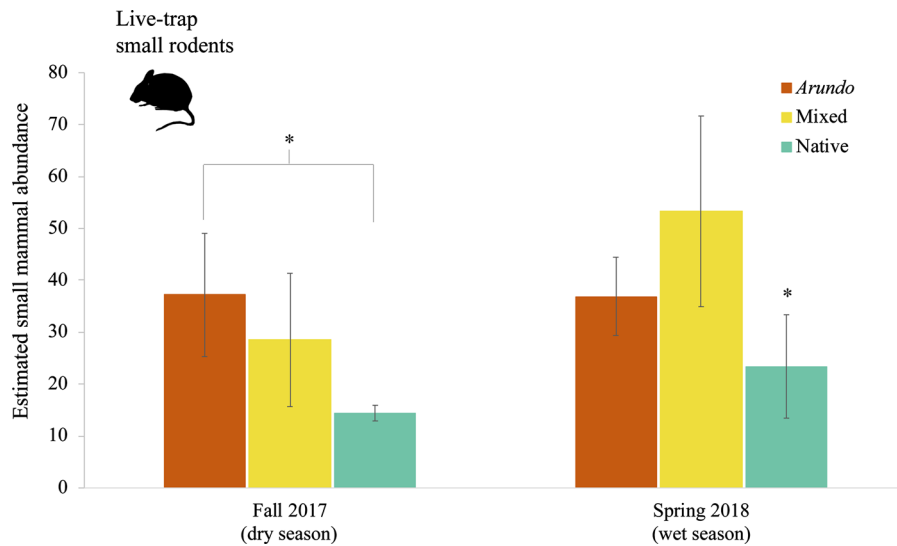
Fig. 3 Estimated small mammal abundance based on best models (Table S12) from mark-recapture data in Fall 2017 and Spring 2018. Habitat type is denoted by color: *Arundo* (orange), mixed (yellow), and native (blue-green). The error bars represent the 95% confidence intervals. Significance is indicated with asterisks (*). There was a significant difference ($\alpha = 0.05$) between the estimated small mammal abundance in native and *Arundo* habitat in 2017, and a significant difference between native habitat and *Arundo* and mixed habitat in 2018

(2017 = 14.4, SE = 0.7; 2018 = 23.4, SE = 4.7). As opposed to the camera trap data, the two-sample t-test on the live-trap data found a significant difference between native and *Arundo* (Table S13; $p < 0.01$) for 2017, and native and *Arundo* and native and mixed (Table S14; $p = 0.0317$ and $p = 0.0377$ respectively) for 2018 (Fig. 3).

Discussion

We have demonstrated that overall the invasive plant *Arundo donax* reduces carnivore use of habitat in a southern California riparian corridor. *Arundo* can significantly alter habitat structure by forming dense, monotypic stands, which have been found to decrease abundance and diversity of native taxa, such as arthropods, birds, and bats (Herrera and Dudley 2003, Kisner 2004, Orr et al. in review). Our results show significantly lower carnivore use of habitat in the high-density *Arundo* stands, and even the presence of *Arundo* in a patch (i.e. in the mixed patches) was observed to decrease likelihood of carnivore use in the pooled carnivore data.

However, we also found evidence that the interaction between *Arundo* invasion and carnivore habitat use are more complex than the pooled species results would suggest. When we modeled multi-season occupancy for coyotes and bobcats individually, interpreted in this study as probability of habitat use (see *Occupancy model* in Methods section), we found less influence of habitat type than for all carnivore species pooled. Coyotes and bobcats were more likely to use native habitat than *Arundo*, but we didn't find much effect of habitat type in the models. The habitat model did have enough support ($\geq 30\%$) to potentially indicate a role for habitat type in predicting use for both species, but it was not a strong pattern. Habitat type had slightly more support in the coyote model than the bobcat model, which could be due to the greater sample size of detections for coyotes.

While we did not find much difference between the coyotes and bobcats in the multi-season model, the single-season occupancy models revealed a strong influence of habitat type on coyote habitat use in 2017 and no pattern for bobcats in any year. In 2017, coyotes had a much higher probability of using native patches than *Arundo*, and presence of *Arundo* was found to be an important predictor of habitat use. In contrast, the bobcat models showed very little to no effect of *Arundo* on predicting use of habitat for all years. The mechanisms driving this difference for
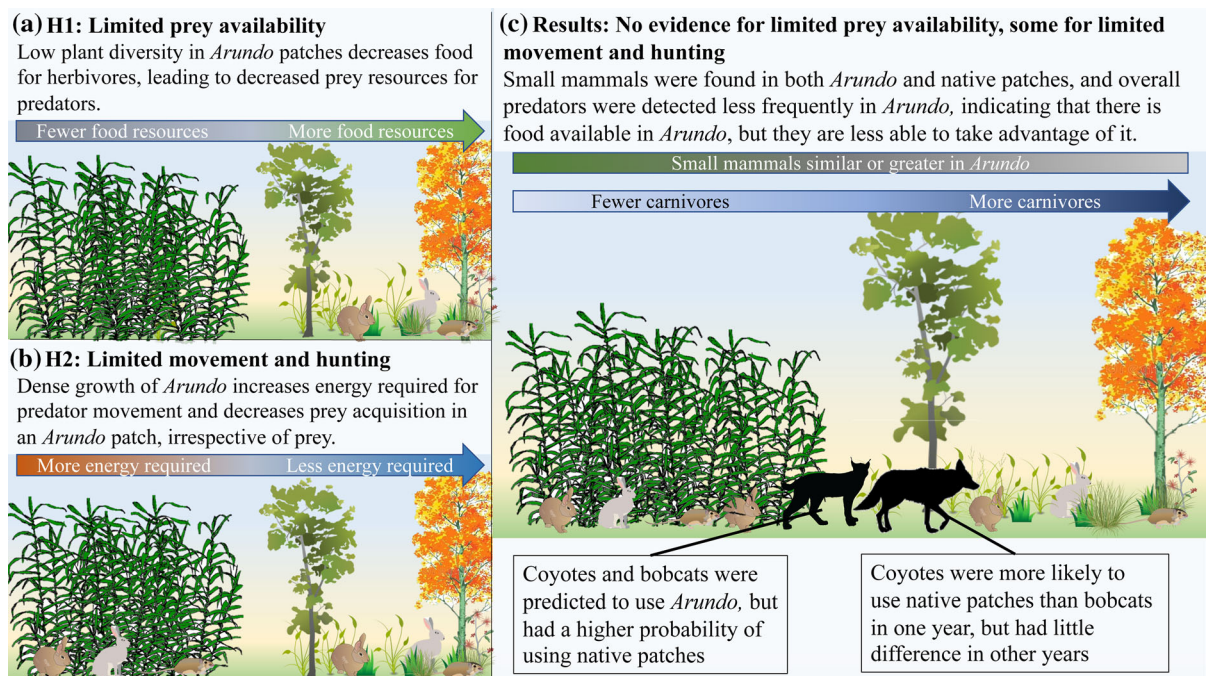
(a) H1: Limited prey availability
Low plant diversity in *Arundo* patches decreases food for herbivores, leading to decreased prey resources for predators.

Fewer food resources　　　　More food resources

(b) H2: Limited movement and hunting
Dense growth of *Arundo* increases energy required for predator movement and decreases prey acquisition in an *Arundo* patch, irrespective of prey.

More energy required　　　　Less energy required

(c) Results: No evidence for limited prey availability, some for limited movement and hunting
Small mammals were found in both *Arundo* and native patches, and overall predators were detected less frequently in *Arundo*, indicating that there is food available in *Arundo*, but they are less able to take advantage of it.

Small mammals similar or greater in *Arundo*

Fewer carnivores　　　　More carnivores

Coyotes and bobcats were predicted to use *Arundo*, but had a higher probability of using native patches

Coyotes were more likely to use native patches than bobcats in one year, but had little difference in other years

Fig. 4 **a** and **b** Diagram of the two hypothesized mechanisms explaining the result that the invasive plant *Arundo donax* decreases carnivore use of habitat. **c** Outcome of the study as it relates to the two proposed mechanisms: no evidence was found to support limited prey availability in *Arundo*, yet still fewer carnivores were found in *Arundo* than native

coyotes in 2017 were not directly explored. The first year of sampling (2016) was carried out during a long drought in this region, and the rains of 2017 brought the first major flood to the SCR in several years (542 mm of rainfall). Possibly, this influx of water altered the habitat such a way as to alter coyote behavior, such as increasing growth and density of *Arundo* to make movement more difficult (Bell 1997) or increasing availability of food resources outside of *Arundo*.

The results from 2017 indicate *Arundo* might be a more important predictor of habitat use for coyotes than for bobcats, possibly because the two species have different body sizes and hunting modes. Coyotes tend to have larger body sizes on average, whereas bobcats are often smaller in stature, and larger body size could increase the energetic cost of moving through dense vegetation (Litvaitis and Harrison 1989). Bobcats have been found to prefer closed habitat with dense vegetation, and although *Arundo* tends to have lower habitat heterogeneity (Bell 1997), the dense stands could provide sufficient cover for an ambush predator (Tucker et al. 2008). On the other hand, coyotes, as coursing predators, would likely have lower success chasing prey through *Arundo* than native habitat, and coyotes generally show a preference for open habitat in which the cost of movement is low (Murray et al. 1995; Thibault and Ouellet 2005).

To help determine what might be driving the decreased use of *Arundo* habitat by carnivores, we examined the hypothesized mechanism of limited prey availability in *Arundo* by focusing on small mammals, which are often important sources of nutrition for carnivores (Delibes et al. 1997; Fedriani et al. 2001). There are also a number of non-mammalian small-bodied organisms that could be potential prey for carnivores in this region which were not considered in this study. If prey limitation were the principle driving mechanism behind decreased carnivore use of *Arundo*, we would expect to see lower small mammal abundance in *Arundo* habitat patches. Instead, we saw similar or even elevated levels of small mammal abundance and habitat use in *Arundo*, which indicates there is small mammal prey available for the predators and that food might not be the key factor limiting carnivore use of *Arundo* patches. It seems small mammals are able to utilize *Arundo* patches to a similar degree or perhaps more than native, according

to our live-trapping results, which suggests there could be lower predation pressure in *Arundo* patches, thereby potentially acting as a refuge for small mammals. Carnivore use of native patches is consistently predicted to be higher than *Arundo*, particularly in the pooled species analyses, which also could support the idea of decreased predation pressure in *Arundo*.

As we do not see less small mammal prey in *Arundo* patches, we have evidence to reject the limited prey hypothesis and find some support for the limited mobility mechanism to explain the decreased use of *Arundo* habitat by carnivore species (see Fig. 4 for summary of mechanisms and results). The dense vegetation could be increasing difficulty of movement and prey acquisition for carnivores, to a degree that some small mammal prey species might be benefiting by occupying *Arundo* patches. We had expected to see a difference by hunting mode or body size yet did not find a significant difference between bobcats and coyotes. The weak difference in our multi-season occupancy models and increased influence of *Arundo* on coyote habitat use in 2017 could indicate that carnivores with coursing-style hunting modes are at more of a disadvantage in the *Arundo* patches, but this cannot be said with any certainty.

There are many other factors that could be contributing to the variation in mammal habitat use. This study focused solely on the percent of *Arundo* in habitat patches and did not take into account fine-scale vegetation differences or differences in the surrounding matrix, which very likely would also affect carnivore movement patterns. As this study focused on the patch scale, further research at the landscape level is necessary to determine how the network of invaded and natural patches scale up to alter carnivore movement through this riparian corridor.

The evidence from this study reveals complexities and further negative consequences of *Arundo* invasion, and there may be similar dynamics occurring in other sites invaded by *Arundo* around the world. *Arundo*, and potentially other large-statured invasive grasses (e.g. *Phragmites australis* and *Phalaris arundinacea*), can have variable effects on native carnivores, likely changing community composition in sensitive riparian habitats. Though *Arundo* habitat was used less than native for coyotes and bobcats, the fact that it was used by both species could indicate that even invaded sites in riparian corridors have some

value for carnivore conservation. More importantly, these results also emphasize the importance of *Arundo* removal and habitat restoration in riparian zones, and the prevention of further spread of invasive plants like *Arundo*. The consequences of altering use of habitat and predator–prey dynamics in invaded habitat could be widespread, adding to already-identified problems of altered species interactions in these regions. The results from this study can help highlight potential ecological and trophic consequences for large-statured invasive grasses in this context and more generally extend our understanding of the diversity of effects that plant invasions can have on ecosystem and community dynamics.

Author's contribution MHM, DO, and DJM contributed to the conception and design of the field experiment. MHM and DO performed the field work. MHM analyzed the data and wrote the manuscript, with contributions from DO and DJM.

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