




RESEARCH ARTICLE

Predation risk can modify the foraging behaviour of frugivorous carnivores: Implications of rewilding apex predators for plant–animal mutualisms

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Abstract

1. Apex predators play key roles in food webs and their recovery can trigger trophic cascades in some ecosystems. Intra-guild competition can reduce the abundances of smaller predators and perceived predation risk can alter their foraging behaviour thereby limiting seed dispersal by frugivorous carnivores. However, little is known about how plant–frugivore mutualisms could be disturbed in the presence of larger predators.
2. We evaluated the top-down effect of the regional superpredator, the Iberian lynx *Lynx pardinus*, on the number of visits and fruits consumed by medium-sized frugivorous carnivores, as well as the foraging behaviour of identified individuals, by examining the consumption likelihood and the foraging time.
3. We carried out a field experiment in which we placed Iberian pear *Pyrus bourgaeana* fruits beneath fruiting trees and monitored pear removal by frugivorous carnivores, both inside and outside lynx ranges. Using camera traps, we recorded the presence of the red fox *Vulpes vulpes*, the Eurasian badger *Meles meles* and the stone marten *Martes foina*, as well as the number of fruits they consumed and their time spent foraging.
4. Red fox was the most frequent fruit consumer carnivore. We found there were fewer visits and less fruit consumed by foxes inside lynx ranges, but lynx presence did not seem to affect badgers. We did not observe any stone marten visits inside lynx territories. The foraging behaviour of red foxes was also altered inside lynx ranges whereby foxes were less efficient, consuming less fruit per unit of time and having shorter visits. Local availability of fruit resources, forest

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coverage and individual personality also were important variables to understand visitation and foraging in a landscape of fear.

- Our results show a potential trophic cascade from apex predators to primary producers. The presence of lynx can reduce frugivorous carnivore numbers and induce shifts in their feeding behaviour that may modify the seed dispersal patterns with likely consequences for the demography of many fleshy-fruited plant species. We conclude that knowledge of the ecological interactions making up trophic webs is an asset to design effective conservation strategies, particularly in rewilding programs.

KEYWORDS

fleshy fruit, Iberian lynx, Iberian pear, individual variability, landscape of fear, mesopredator release, seed dispersal, trophic cascade

1 | INTRODUCTION

A trophic cascade occurs when predators trigger a reverberating effect across lower trophic levels in food webs (Estes et al., 2011; Ripple et al., 2016). Apex predators are at the top of trophic webs and can lead to top-down effects on the abundance and behaviour of prey populations, critically influencing ecosystem structure and functions (Schmitz, 2006; Winnie & Creel, 2017). Recent recovery and rewilding processes involving large carnivores world-wide (Chapron et al., 2014) have increased the attention of ecologists and conservation practitioners towards those cascading effects (Ritchie et al., 2012). Some studies have revealed direct killing by carnivores causes reductions in herbivore population sizes, which translates into positive effects for plants (Ripple & Beschta, 2007, 2012b). Nonetheless, trophic cascades can also occur by non-lethal interactions through a behavioural change in response to a perceived predation risk (Schmitz et al., 2004) and the subsequent anti-predatory behaviour modifies the ecosystem functioning (Ripple & Beschta, 2004). The most evident cascading effects on plants are mediated by herbivores (Ripple & Beschta, 2012a, 2012b), but little is known about the potential top-down effects of apex predators on plant–carnivore mutualisms.

Predator–prey interactions usually involve large carnivores and herbivores; however medium-sized carnivores (i.e. mesocarnivores) can also play the role of prey when they coexist with larger predators, known as superpredators (Holt & Polis, 1997). Superpredators often control population abundances of smaller predators by intra-guild predation or other types of antagonistic interactions, resulting in competition for shared resources (Polis et al., 1989). The global extirpation of apex predators (Wolf & Ripple, 2018) has shifted many ecosystems to a state of mesopredator release (Crooks & Soulé, 1999). Apex predators promote a landscape of fear—an animal's perception of spatial variation in predation risk (Gaynor et al., 2019)—that not only alters abundance, but also the foraging behaviour of mesopredators (Laundré et al., 2010; Pasanen-Mortensen et al., 2013). For instance, Haswell et al. (2018) found that foxes responded to perceived predation risk by being less efficient foragers and spending

less time visiting food patches. Similarly, Leo et al. (2015) identified non-foraging behaviours, such as resting, were less frequent under predation risk by foxes. Food patches which offer fewer resources but a low exposure to predation risk may be the optimal foraging sites even if the available resources are potentially more challenging to obtain (Brown et al., 1999; Laundré et al., 2010). According to the optimal foraging theory (Charnov, 1976), predation risk can select more efficient or cautious foragers that modify their foraging behaviour due to the fear of larger carnivores (Eccard et al., 2020; Toscano et al., 2016) resulting in a trophic cascade on the resources exploited (Suraci et al., 2016).

Trophic cascades can also shape ecosystem functions that involve plant–animal interactions other than herbivory, such as seed dispersal (Kurten, 2013). Ripple et al. (2014) were pioneers in this regard after wolves were reintroduced in Yellowstone. They found seed dispersal by grizzly bears increased due to a less abundant population of elks competing with bears for fruit resources. This finding indicates the value of opportunistic foraging by carnivores (Fedriani et al., 1999) and highlights their role in ecosystem functioning as agents of seed dispersal (Schupp et al., 2010). Frugivorous carnivores have functional differences with other main groups of seed dispersers that make them especially effective in this key mutualism (Escribano-Ávila et al., 2014; González-Varo et al., 2015). Carnivores can move many seeds over long distances and increase the probability of seed germination (Escribano-Ávila et al., 2013; Traveset & Verdu, 2002). Despite literature studying the implications for seed dispersal of the lack of key frugivore–plant interactions is growing recently, the loss of big-sized frugivores has been usually linked to defaunation (de Paula Mateus et al., 2018; Fedriani et al., 2020) rather than to reintroductions of superpredators.

In the Mediterranean ecosystems of Southern Spain, the Iberian lynx *Lynx pardinus* is the largest regional predator and plays the role of superpredator (Fedriani et al., 1999). This feline was near extinction in the 1990s as a consequence of direct exploitation, habitat fragmentation and human-assisted spread of diseases affecting its main prey (Rodríguez & Calzada, 2015). The Iberian lynx is still one of the most endangered feline species in the world (Rodríguez &

Calzada, 2015). However, populations have recently increased and are currently estimated at 855 individuals (MITECO, 2019). The recovery of this superpredator is due to several conservation efforts mainly focused on prey and habitat management, captivity breeding, reintroductions and enhancement of the genetic diversity of extant populations (Simón et al., 2012). Lynx cause direct decreases in mesopredator abundance and alter their habitat use (Sarmento et al., 2021), and the suppression of mesopredator release has positive effects on small prey species (Jiménez et al., 2019). Nevertheless, mesocarnivores are important seed dispersers in Mediterranean ecosystems (Herrera, 1989), and a decrease in their abundance or alterations to their foraging behaviour could negatively influence their mutualistic interactions with plants (Carreira et al., 2020; Pegman et al., 2017). Thus, to shed light on whether the Iberian lynx may induce a trophic cascade on Mediterranean fleshy-fruited plants, we performed a field experiment to study the foraging behaviour of the carnivore community in areas where the Iberian lynx is present and compared to areas where this apex predator is extinct. We hypothesized that the presence of lynx would affect: (a) the number of visits to fruit trees and the number of fruits consumed by mesocarnivores at constructed fruit depots and (b) the foraging behaviour of the main frugivorous mesocarnivore. In particular, we expected that the presence of lynx will decrease the number of visits of mesocarnivores and, consequently, the amount of fruit consumed. In addition, we expected frugivorous mesocarnivores to be less efficient under predation risk and to make shorter visits.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted during the autumn (October–November) of 2019 in Sierra de Andújar Natural Park (38°14′27.71″N, 4°4′45.03″W, near 740 km²). The annual average temperature (~18°C) and rainfall (~700 mm) are typical for Mediterranean climate areas (data from Andújar meteorological station, AEMET Open Data Repository, 2020). The altitude ranges between 400 and 800 m. The study area is located within extensive private lands where large wild ungulates are frequently hunted, but small game hunting and predator control is unusual or absent. Vegetation is dominated by Mediterranean shrubland and holm oaks *Quercus ilex*. Some of the fleshy-fruited species present include: the strawberry tree *Arbutus unedo*, the mastic *Pistacia lentiscus* and the Iberian pear tree *Pyrus bourgaeana*.

This Natural Park is home to one of the largest Iberian lynx population and was the last refuge together with Doñana for this species in the 1990s decade (Simón et al., 2012). The area does not count with lynx reintroduced populations; however, lynx has expanded its distribution range over the last 20 years, due to several conservation efforts (Simón et al., 2012). Despite its recovery, Iberian lynx home ranges are heterogeneously distributed throughout the area which offered the opportunity to select otherwise similar areas that

differ in the presence/absence of lynx. We studied distribution and abundance of lynx from camera-trapping surveys before designing this experiment (see Table S2; Burgos et al., unpubl.) in order to select these locations. Lynx coexist with a rich community of mesopredator species in the study area, including frugivorous carnivores such as the red fox *Vulpes vulpes*, the stone marten *Martes foina*, the common genet *Genetta genetta* or the Eurasian badger *Meles meles*. Frugivorous carnivore abundances are lower inside lynx ranges (with the exception of the Eurasian badger, see Table S2), due to predation of the mesocarnivores populations by the Iberian lynx (Jiménez et al., 2019).

2.2 | Study plant species

We selected the Iberian pear as the fruit study species because this plant is mainly dispersed by frugivorous carnivores (Fedriani & Delibes, 2013), which ingest whole ripe fruits. This causes only minor mechanical damage to seeds (Fedriani & Delibes, 2009b). Foxes and badgers are long-distance legitimate dispersers of Iberian pear despite being less abundant than other frugivores such as ungulates (Fedriani et al., 2010; Fedriani & Delibes, 2009b). The wild boar *Sus scrofa* only occasionally disperses seeds, while the red deer *Cervus elaphus* and the fallow deer *Dama dama* act as seed predators. Rodents, birds and rabbits function primarily as seed predators or pulp feeders (Fedriani et al., 2012; Fedriani & Delibes, 2009b; Fedriani & Delibes, 2013).

This small tree produces fleshy pomes (2–3 cm diameter; ~9.5 g wet weight) (Fedriani & Delibes, 2009b) with a high sugary and water-rich pulp content (Herrera, 1987). Fruits fall ripe during September–November and contain one to five viable seeds (Fedriani & Delibes, 2009b). The Iberian pear is a predictable food resource in the area, producing a large number of fruits (from 100 to >1,000 fruits per tree). It has an aggregated distribution, linked to a seed dispersal pattern induced by mammals, with seed clustering and some seedling establishment beneath mother trees (Fedriani et al., 2010; Fedriani & Delibes, 2009b). In Sierra de Andújar, Iberian tree clusters occurred in very low densities (even lower than in other Mediterranean areas such as Doñana National Park; <1 individual/ha; Fedriani et al., 2010) and were composed of three to 19 trees. Pear trees are relatively isolated from other fruiting species, growing most often in substrates lacking vegetation or coexisting with small-fruited shrub species such as *P. lentiscus* whose fruits are seldom consumed by mesocarnivores (Herrera, 1989).

2.3 | Sampling design

Our experiment compared frugivorous carnivores foraging on pear fruits in areas where the Iberian lynx was present or absent. We selected the area with lynx based on camera-trapping data taken in a previous study (Table S2; Burgos et al., unpubl.), where we recorded images of at least two territorial lynx couples. We placed fruit

depots beneath 30 adult pear trees. Fifteen depots were located inside lynx distribution range, and the remaining 15 were used as controls outside lynx territories. Due to the patchy and scarce distribution of the Iberian pear tree, we distributed the fruit depots based on the availability of trees. The distance from a pear tree in lynx range to a control tree ranged from 4.6 to 19.3 km. We selected isolated trees and clustered trees (both within and outside lynx territories) to have a higher and representative sample from the wild distribution of the Iberian pear. We placed eight fruit depots beneath isolated trees (four of them within and four outside lynx territories) and the rest of the depots ($n = 22$) were placed in clusters ($n = 11$). The number of depots per cluster varied depending on its size and the number of trees that comprised the patch, ranging from one to three. We considered isolated trees and independent clusters as those located over a 100 m away from the nearest pear tree (see Figure 1).

Each fruit depot was comprised of 30 ripe fruits within a 1 m side squared plot. Fruits were set regularly in six lines (five fruits per line) about 10 cm apart (Figure 1). We placed a camera trap (Scoutguard SG562-C; white led) on the pear tree trunk at the height of 60 cm with a slope of 45 degrees. We programmed the cameras to record three images per second when movement was detected, with a minimum time delay (0 s) between consecutive records to maximize the number of images taken per visit. The experiment lasted 15 consecutive days. We visited each camera trap site every 5 days to refill the fruit depots. We reached an overall effort of 437 trap-days in which cameras were working and offered 2,700 Iberian pear fruits during the experiment.

2.4 | Data collection

We processed a total of 130,269 images taken by camera traps and recorded the species, the date and the hour of each visit. The number of fruits consumed in each visit was estimated by comparing every image with the previous one to count the number of fruits left. We distinguished the fruits offered from the fruits fallen by

marking all offered fruits with a white natural thread. The time spent per visit was calculated as the difference between the time of the first and the last image from each visit. Visits were considered independent events when separated by a period greater than 30 min (Linkie & Ridout, 2011). When possible, different red foxes within the same image were identified and considered separately. Foxes have particular fur marks that often make them easily recognizable, mainly in the legs, face and tail (Sarmiento et al., 2009; Figure S1). We identified individual foxes in 80% of all fox events in cameras placed in lynx territories and 74% outside these. Two experts identified individually 10 foxes outside lynx ranges and four inside by consensus.

We accounted for habitat and fruit availability to assess the possible confounding effects of landscape structure and food resources. The crop size of focal Iberian pear trees was estimated (both isolated and within cluster). We counted the number of individual fruiting trees in the clusters and visually estimated the individual crop size. We transformed our data on crop size into a logarithmic fruit abundance index (FAI): 0 = no fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1,000; 4 = 1,001–10,000; and 5 > 10,000 (see Saracco et al., 2004). The crop size of isolated trees was calculated by adding up the number of fruits on the canopy to the number of ripe fruits fallen on the ground every time we replenished the fruits in the depots (three times in total). Similarly, we calculated the crop size of Iberian pear clusters by adding up the average number of fruits per individual tree to the number of ripe fruits on the ground inside the cluster. We also recorded the forest cover inside a 100-m circular buffer around each isolated tree where we located the fruit depots. For tree clusters, we used a 100-m buffer around a minimum convex polygon (MCP) including all pear trees within the cluster (Figure 1). We digitized the surface covered by forest from a high-resolution (0.5 m) orthophotography and calculated the percentage of forest cover within buffers (IGN, 2016).

All camera-trapping surveys were permitted by the land owner and manager and the Territorial Delegation of Environment of Jaén with expedient number 201899900431971. Ethical approval was not required for this study.

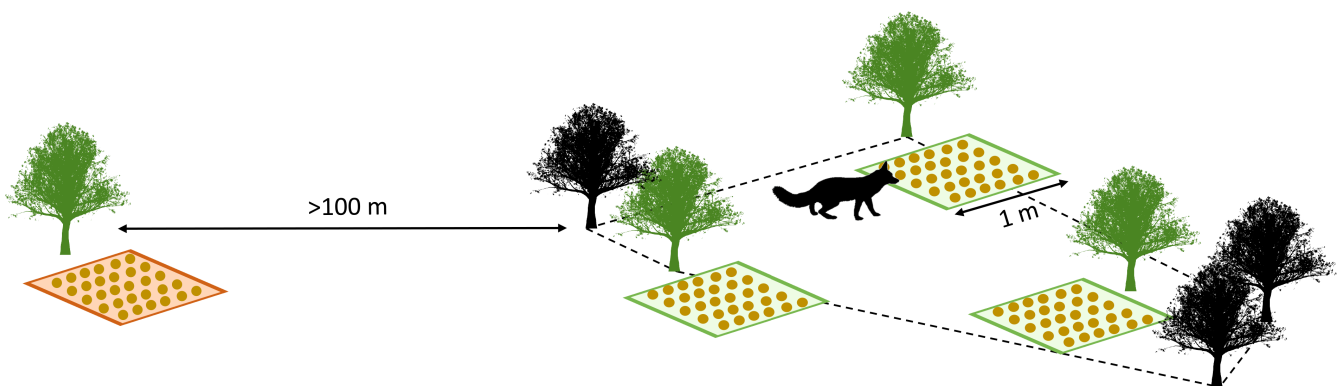


FIGURE 1 Field sampling design showing the depots of fruits beneath isolated Iberian pear trees (orange squares) and beneath clustered trees (green squares). Green trees show Iberian pear trees selected to locate the offers and camera traps. The dashed line shows the polygon-shaped linking trees in the clusters according to the method of minimum convex polygon

2.5 | Statistical analysis

We built GLMMs to evaluate the effect of Iberian lynx presence on the number of visits, fruit consumption and foraging behaviour of frugivorous carnivores in the fruit depots. We built a GLMM for the following response variables: (1) number of visits, (2) proportion of fruits consumed in the fruit depots, (3) consumption/non-consumption of fruits in each visit, (4) fruits consumed per second in each visit and (5) time spent per visit in seconds. We used lynx presence/absence, crop size and forest cover as fixed effects plus the interaction terms crop size \times lynx and forest cover \times lynx. Because the number of stone marten visits and amount of fruits consumed by badgers were both low ($n = 15$ and $n = 31$ respectively), we only used the red fox and badger data to analyse the number of visits (first response variable) and only the red fox data for the rest of response variables. We also added the species of carnivore for the number of visits as a fixed factor and as an interaction term with lynx presence, crop size and forest cover. The models for the third, fourth and fifth response variables did not include interaction terms to avoid overfitting due to our low sample size (following Matuschek et al., 2017). For these response variables, we used a reduced dataset that included only the fox visits that were successfully identified ($n = 310$). We only included the visits in which the identified foxes consumed fruits for the fruits consumed per second ($n = 106$), and the visits that lasted between 1 s and 15 min for the time per visit ($n = 161$). We limited the time interval of the visits because we recorded many visits with very low (1 s) and very high values (>15 min) that hampered model convergence and fit. Cluster ($n = 19$) was added as random factor in all models including isolated trees, and the identity of red foxes ($n = 14$) was added as (partially) crossed random effect for the third, fourth and fifth response variables. The number of days that the camera traps were active was added as an offset in all models because some cameras failed in certain days. We used Poisson errors for the first response variable, binomial for the second and third and Gamma for the fourth and fifth. We inspected diagnostic graphs to assess normality and homoscedasticity of residuals. We checked the lack of spatial autocorrelation among clusters with Moran's Index for all the response variables (Table S3).

Model selection on GLMMs was performed comparing models which contained all the possible combinations of fixed effects and interaction terms given above with models without our variable of interest, lynx presence/absence. We selected the best-fitting model that minimized the second-order Akaike information criterion (AICc). If only one model had an AICc > 2 with respect to the rest of the models, it was considered the best model. When differences between several models had an AICc < 2.0, we considered these models as set of confidence models with similar statistical support and we calculated the Akaike weights (Burnham & Anderson, 2002). We carried out post hoc simple-slope pairwise comparisons to estimate the coefficients of the interaction terms. We calculated the marginal and conditional coefficient of determination (pseudo- R^2) for the selected models (Nakagawa et al., 2017).

All the statistical analyses were conducted in R (version 3.6.1; R Core Team, 2019). We used R base functions and specialized packages (LME4 v.1.1-27.1 for GLMMs: Bates et al., 2020; MuMIn

v.1.43.17 for pseudo- R^2 and model selection: Barton, 2013; APE v.5.5 for Moran's Index: Paradis et al., 2020; and EMMEANS v.1.6.3 for post hoc comparisons: Russell et al., 2021).

3 | RESULTS

We recorded 2,370 independent visits to the fruit depots in which the frugivores consumed 69% of the Iberian pear fruits offered. Fruit depots were visited by 14 mammal species and 10 bird species, but only 11 species consumed fruits (Table S1). Seed predators (ungulates) were the group of frugivores which consumed the most fruit, followed by the legitimate seed dispersers, the frugivorous carnivores (Table S1). We did not find differences between predation risk scenarios (i.e. lynx presence vs. lynx absence) both for visitation ($\chi^2 = 2.33$; $df = 1$; $p = 0.13$) and consumption ($\chi^2 = 0.60$; $df = 1$; $p = 0.44$) considering the whole frugivores assemblage (Figure S2).

3.1 | Visits and quantity of consumed fruits by carnivores

We recorded 458 visits of three species of frugivorous carnivores in the fruit depots (Table S1). The red fox showed the highest percentage of visits (87%), while the badger (10%) and the stone marten (3%) were much less frequent. Each carnivore species showed a different pattern of visitation to fruit depots. Fox visited fruit depots much more frequently in areas outside lynx ranges than inside ($M \pm SE$: 2.18 ± 0.46 , 6.96 ± 1.22) with about 70% of fox visits occurring outside lynx territories. On the contrary, badgers visited fruit depots located within lynx territories more frequently (0.73 ± 0.20 in lynx presence and 0.31 ± 0.11 in lynx absence scenario). No visits were recorded for the stone marten when lynx was present (0.33 ± 0.13 in lynx absence) (Figure 2a).

Carnivores consumed 20.4% ($n = 380$) of fruits removed from the depots (Table S1). Red fox consumed by the far the highest percentage of fruits (90.79%), whereas badgers and martens consumed minor quantities (8.16% and 1.05% respectively). The proportion of Iberian pear fruits consumed by foxes per depot was $9.7 \pm 0.03\%$ ($n = 213$) and $15.7 \pm 0.03\%$ ($n = 132$) in presence and absence of lynx respectively. Thus, overall 38% less fruit was consumed within lynx territories. Badgers consumed fruits where the Iberian lynx was present in a greater proportion ($1.4 \pm 0.01\%$) than where the lynx was absent ($0.8 \pm 0.01\%$) (Figure 2b). The proportion of fruits consumed per depot by stone marten was $0.3 \pm 0.002\%$, and all the consumption events took place outside lynx ranges (Figure 2b).

3.2 | Visitation modelling of foxes and badgers

We obtained one best model with $\Delta AICc < 2$ which included lynx presence/absence, species of carnivore, crop size and forest

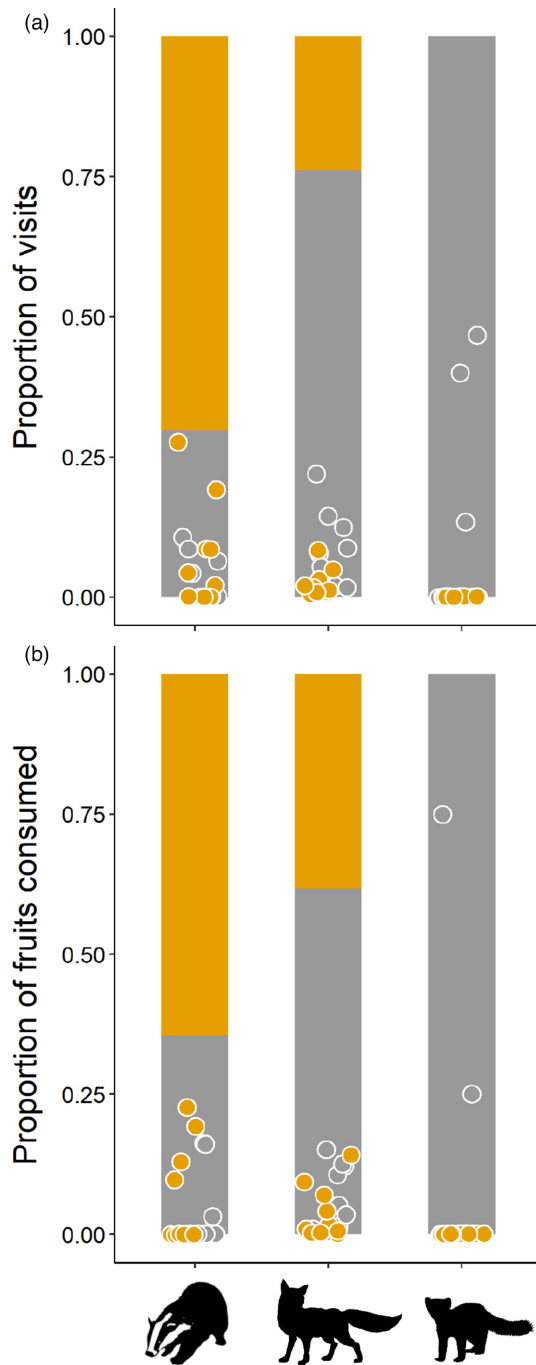


FIGURE 2 Proportion of the number of visits to fruit depots (a) and proportion of fruits consumed (b) by the three species of carnivore mammals that consumed pear fruits. First silhouette refers to the Eurasian badger *Meles meles*, second refers to the red fox *Vulpes vulpes* and the third to the stone marten *Martes foina*. Orange refers to depots inside Iberian lynx ranges and grey represents depots outside. Circles denote tree cluster level observations

cover and the interaction terms lynx \times species \times forest cover and lynx \times crop size (Tables 1; Table S4). Post hoc comparisons showed that the carnivores most often visited pear trees with larger crop size where the lynx was absent (CS: 560.48 ± 54.55 ; coeff. = 0.73, $SE = 0.25$). However, we found the opposite relationship when they coexisted with lynx (CS: 927.57 ± 307.03 ; coeff. = -0.16, $SE = 0.07$).

TABLE 1 GLMMs for the number of mesocarnivore visits to experimental depots and for the proportion of pear fruits consumed. The list of candidate models within $2 \Delta AICc$ is shown. K, number of parameters in the model; Loglik, log-likelihood; W, Akaike's weight; R_c^2 and R_m^2 give conditional and marginal proportion of variance explained

Response	L	Sp	C	FC	Sp \times C	Sp \times FC	Sp \times L	L \times FC	L \times C	L \times Sp \times C	L \times Sp \times FC	K	Loglik	AICc	$\Delta AICc$	W	R_c^2	R_m^2
(1) No. visits	X	X	X	X	X	X	X	X	X	X	X	11	-296.23	616.03	0	0.76	0.90	0.63
(2) Prop. fruits	X	-	-	-	-	-	-	-	-	-	-	3	-281.40	569.09	0	0.26	0.27	0.08
	-	-	X	-	-	-	-	-	-	-	-	3	-281.88	570.05	0.95	0.16	0.27	0.01
	-	-	-	X	-	-	-	-	-	-	-	3	-282.05	570.38	1.28	0.14	0.27	0.01
	X	-	X	-	-	-	-	-	-	-	-	4	-281.06	570.60	1.51	0.12	0.27	0.08

Abbreviations: C, crop size (fruits/tree or cluster); FC, forest cover (%); L, lynx presence or absence; Sp, mesocarnivore species (fox and badger). The multiplicative symbol (\times) indicates an interaction term.

We also found that foxes visited more often pear trees with higher forest cover when lynx was present, but we did not find this relationship for badgers (Figure S3).

3.3 | Fruit consumption models by foxes

We obtained four models similarly plausible according to AICc and none of them included interaction terms (Table 1). The variables lynx presence/absence and crop size were included in two models each and the variable forest cover was included only in one model (Table 1). Crop size and forest cover had a positive effect on the proportion of fruit consumed by foxes (Table S4).

3.4 | Foraging behaviour modelling of identified foxes

We obtained six models with $\Delta\text{AICc} < 2$ for the fruit consumption/non-consumption response (Table 2). The variables lynx presence/absence, crop size and forest cover were included in three models each (Table 2). The number of successful consumption events were similar to non-consumption events in lynx presence, but events without consumption were higher in the absence of lynx (Figure 3a). The probability of consuming fruit was positively related to crop size and negatively related to forest cover (Table S4). The proportion of random effects variance in the consumption probability attributable to differences among fox individuals was higher than that attributable to differences among clusters (Table S4).

For the fruits consumed per second in each visit, we obtained one best model with $\Delta\text{AICc} < 2$ which contained only the variable lynx presence/absence (Table 2). We found that foxes consumed less fruit per second when they coexisted with lynx (Figure 3b). Fox identity was the random effect which explained almost the entire proportion of residual variance in the model (Table S4).

For the time spent per visit, we obtained four models with similar plausible AICc (Table 2). The variables lynx presence/absence and crop size were included in three models each and the forest cover was included only in one model (Table 2). Foxes spent less time in visits to pear trees inside lynx territories than outside lynx ranges (Figure 3c). We found that the crop size had a positive effect on the time per visit while the forest cover had a negative effect (Table S4). The proportion of the explained residual variance by random effects was bigger for the tree cluster than for the fox individual (Table S4).

4 | DISCUSSION

The ecological interactions among the apex predator, frugivorous carnivores and a fleshy-fruited tree in Southern Spain suggest a trophic cascade induced by a predation risk scenario. Red fox—a legitimate seed disperser for the Iberian pear (Fedriani & Delibes, 2009b)—was the main fruit consumer among carnivores, but in territories with the presence of an apex predator, a smaller number of foxes conducted fewer visits to pear trees, consumed less fruit and spent less time searching for fruit. Although foxes had less opportunity to feed when under predation risk, they consumed fruits less efficiently. These results suggest the presence of lynx reduces the abundance of foxes and alters their foraging behaviour, which could inhibit the efficacy of foxes as seed dispersers. Overall, the results support our hypothesis that the Iberian lynx can affect a key plant–animal mutualism, that could result in a negative cascading effect on seed rain of plant species whose seed dispersal depends on mammal carnivores.

4.1 | Lynx differentially affect mesocarnivore visitation

Frugivorous mesocarnivores actively search for Iberian pear fruits because these are a predictable and valuable resource in

TABLE 2 GLMMs within 2 ΔAICc built to explain the foraging behaviour of the main seed disperser, the red fox. K; number of parameters in the model; Loglik, log-likelihood; W, Akaike's weight. R_c^2 and R_m^2 give conditional and marginal proportion of variance explained

Response	L	C	FC	K	Loglik	AICc	ΔAICc	W	R_c^2	R_m^2
(3) C/NC	X			4	-187.79	383.71	0	0.26	0.15	0.03
			X	4	-188.14	384.42	0.70	0.18	0.17	0.01
		X		4	-188.29	384.72	1.01	0.16	0.16	~0
	X	X		5	-187.56	385.32	1.61	0.11	0.15	0.03
	X		X	5	-187.65	385.501	1.78	0.10	0.15	0.03
		X	X	5	-187.71	385.61	1.90	0.10	0.17	0.01
(4) Fruits/s	X			5	159.49	-308.38	0	0.94	0.63	0.02
(5) Time/visit	X	X		6	-1,053.04	2,118.64	0	0.22	0.22	0.08
	X	X	X	7	-1,052.01	2,118.74	0.10	0.21	0.21	0.12
		X		5	-1,054.32	2,119.03	0.38	0.18	0.22	0.02
	X			5	-1,054.55	2,119.50	0.85	0.14	0.18	0.04

Abbreviations: C, crop size (fruits/tree or cluster); FC, forest cover (%); L, lynx presence or absence.

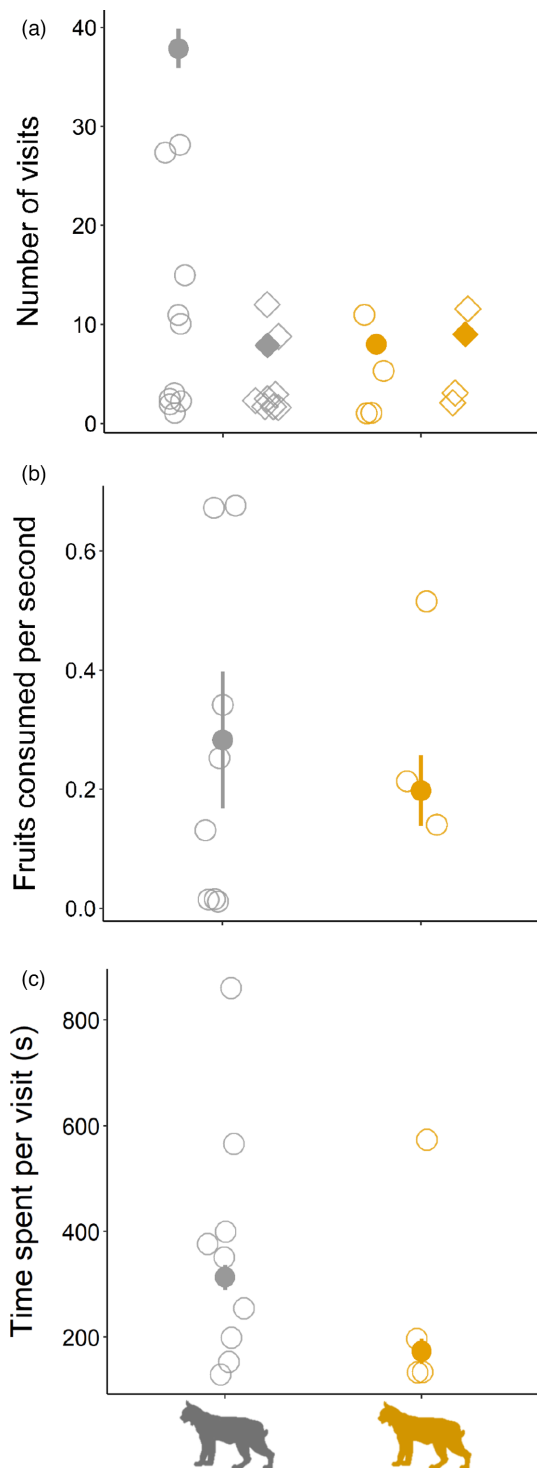


FIGURE 3 Filled circles show the average number of visits without fruit consumption and filled rhombus show the averaged number of visits with consumption (a) by foxes. Filled circles show the number of fruits consumed per second (b) and time spent per visit in seconds (c) by foxes. Bars represent standard errors. Hollow circles refer to the average value found in each fox individual. Orange represents Iberian pear fruit depots inside Iberian lynx ranges and grey represents depots outside lynx ranges

Mediterranean ecosystems (Fedriani & Delibes, 2009a). Therefore, less frequent visits to pear trees under predation risk could be due to lower population abundances, a behavioural avoidance of

agonistic encounters or a combination of both (Carreira et al., 2020; Ripple & Beschta, 2004; Selwyn et al., 2020). We identified far fewer fox individuals and recorded fewer visits in a predation risk scenario, which supports previous work by Garrote et al. (2018), who proposed that in the Doñana National Park, a low frequency of fox visitation to pear fruits was likely related to a high lynx density. Although our best model revealed that lynx presence was an important factor to understand the lower visitation of foxes, we also found that lynx can have a differential effect among meso-carnivores (Fedriani et al., 1999; Jiménez et al., 2019). We found a low number of visits of stone marten and all were recorded in pear trees outside lynx ranges (Jiménez et al., 2019), indicating that the presence of lynx may lead to the virtual extinction of the seed dispersal service provided by stone martens. Conversely, we found more visits of badgers inside lynx territories. Badgers did not seem to show sensitivity to lynx presence, probably due to their larger size and corpulence (Fedriani et al., 1999). The smaller size of martens and foxes relative to the badger could lead them to be easily preyed by a bigger competitor (Virgós et al., 2020) which may explain their low abundance in areas with lynx (see Table S2; Burgos et al., unpubl.).

4.2 | Habitat variables modulate the effect of predation risk on visitation

Foxes and badgers avoided high-production trees inside lynx ranges despite making bigger crop size on average. This behavioural change probably is linked to cost-benefit balance as stated by the optimal foraging theory (Charnov, 1976). Low-production patches could be safer for foraging even if the available resources are potentially more challenging to obtain (Brown et al., 1999). However, we found the opposite relationship when carnivores did not coexist with lynx. In this scenario, carnivores invested foraging efforts to areas where food is easier to find, in accordance with other similar studies (García et al., 2011; Selwyn et al., 2020; Virgós et al., 2010). We found that while badger visits were positively related to forest cover around pear trees in both the presence and absence of lynx, foxes only demonstrated this pattern in the predation risk scenario. As Iberian pear trees were located in low-vegetated areas, foraging in fruit patches with higher forest refuge could be less risky for foxes which live in a landscape of fear (Laundré et al., 2010). In a trophic cascade context, these kinds of behavioural adaptations could determine the spatial patterns, dispersal kernels and effectiveness of seed dispersal for fleshy-fruit plants in the long term (Fedriani et al., 2010; Pegman et al., 2017; Rey & Alcántara, 2014).

4.3 | Lynx presence limits the quantity of fruits consumed by foxes

The main seed disperser of Iberian pear was the red fox. We found that foxes consumed 38% less fruits under a perceived predation

risk by lynx. Despite this reduction being balanced by the consumption of the rest of the frugivore assemblage (see Figure S2), their qualitative seed dispersal effectiveness (*sensu* Schupp et al., 2010) is very low. Carnivore mammals are the legitimate seed dispersers of the Iberian pear (Fedriani & Delibes, 2009b, 2013) while the rest of the frugivores, such as ungulates or lagomorphs, that consumed a relevant proportion of fruits are largely seed predators or pulp feeders (Fedriani & Delibes, 2009b, 2013). Although we did not record many visits of badgers in our study area, this species could potentially balance the loss of seed dispersal by foxes within lynx ranges in areas where they reach greater densities (Fedriani et al., 2020). For example, in Doñana National Park, Iberian pear seeds are mostly dispersed by badgers (Fedriani & Delibes, 2009b), and they are a key species to create new clusters of pear trees away from the tree neighbourhoods (Fedriani et al., 2010).

4.4 | Implications of trophic cascades on plant ecology

The foraging behaviour of foxes was also disturbed by predation risk. We found that when under predation risk, foxes utilized the visits to pear trees to feed on fruits, in contrast to the high proportion of visits without consumption in areas outside lynx distribution range, according to Leo et al., 2015 found. In lynx presence scenario, foxes consumed less fruit per unit of time (i.e. lower efficiency) and their visits to pear trees were shorter, behaviour likely linked to an anti-predatory response (Carreira et al., 2020; Haswell et al., 2018; Selwyn et al., 2020). The combination of a lower fruit consumption and the alteration in the feeding behaviour can cause a cascading effect that disrupts a plant-disperser mutualism (de Paula Mateus et al., 2018; Kurten, 2013). The quantity of dispersed seeds of the Iberian pear could be limited by the presence of lynx because its main disperser (red fox) was less abundant, consumed less fruit and therefore dispersed fewer seeds. Cascading effects on the main disperser could also alter the qualitative seed dispersal (e.g. habitat and microhabitat of seed deposition), affecting plant demography and distribution (de Paula Mateus et al., 2018; Fedriani et al., 2020). As seed dispersal patterns are different among Iberian pear seed dispersers (Fedriani et al., 2010), fewer pear-fox interactions could modify the spatial distribution of pear trees, for instance limiting seed arrival to vacant habitats (e.g. old fields; Fedriani et al., 2020). Moreover, disturbances on the spatial patterns of scat deposition triggered by predation risk could also occur on an intraspecific level as a consequence of behavioural changes (Virgós et al., 2020) and affect seed dispersal delivery contrastingly. For instance, although foxes dispersed fewer seeds in a predation risk scenario, the possibility cannot be ruled out that they move seeds towards safe forest refuges, which could potentially be suitable habitats for seedling establishment of Mediterranean plants (Bustamante et al., 1992).

4.5 | Effects of habitat and individual variation of fox foraging behaviour on fruit consumption

Fruit availability, forest cover and intraspecific variability also explained variation in the foraging behaviour of foxes, in addition to predation risk. Fruit consumption, both the amount of fruits consumed and the probability of consumption, increased with crop size and the visits lasted for a longer time in patches with higher fruit availability, which supports several previous studies about usage intensity of fruit patches (Garcia et al., 2011; Moegenburg & Levey, 2003; Selwyn et al., 2020). Forest cover had a positive effect on the proportion of fruits consumed by foxes, but its effect on the probability of fruit consumption and activity time in the pear trees was negative. This opposite relationship could be due to the different sampling levels used for fruit consumption models (fruit depot) and foraging behaviour models (visit). Mediterranean forest patches can hold a high diversity of food resources for generalist carnivores such as foxes (Cavallini & Volpi, 1996), and they probably also foraged on food items other than fruits, explaining the lower probability of fruit consumption per visit and shorter visits. However, a high forest cover could provide foxes a greater perception of safety (Laundré et al., 2010) allowing them to consume a larger amount of fruits in overall. Moreover, intraspecific variability seems to also be relevant to explain the variation found in the foraging behaviour of foxes such as the likelihood of consuming fruits. As individual variation can also modulate fruit resource exploitation (Araújo et al., 2011; Toscano et al., 2016), more research would be needed to understand how different predation risk scenarios could select certain phenotypes (Eccard et al., 2020; Steinhoff et al., 2020) and how this could in turn alter ecological functions such as seed dispersal.

5 | CONCLUSIONS

In our study area, lynx recovery could reverse the release of the main seed disperser of the Iberian pear, the red fox, by decreasing its abundance and modifying its foraging behaviour. Specifically, foxes visited pear trees less often, consumed less fruit and spent less time searching for fruits under predation risk, resulting in less efficient frugivores. Different elements also affected the foraging behaviour and the decision-making of foxes, such as the availability of food resources, forest refuge and intraspecific variation. Cascading effects from lynx on this key mutualism could alter the demography and spatial structure of the Iberian pear, although a greater abundance of badgers could balance the lack of seeds dispersed by foxes. Thus, fleshy-fruited plants dispersed by medium- and large-sized seed dispersers could experience limitations of their quantitative seed dispersal due to trophic cascades, especially for scarce or endangered plant species. Understanding the ecological interactions among the different levels of food webs is essential to design suitable conservation strategies and predict potential cascading effects in altered ecosystems. Consequently, reintroduction programs of apex predators

should consider trophic cascades as a powerful mechanism, which can alter key ecosystem functions in contrasting ways.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

T.B., E.V., J.M.F. and G.E.-A. conceived the idea and designed the; T.B. and J.H.-H. collected the data; T.B., J.S. and G.E.-A. analysed the data; T.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data will be available in the Dryad Digital Repository upon acceptance. Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.mpg4f4r0q> (Burgos et al., 2022).

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