

RESEARCH ARTICLE

Apex predators can structure ecosystems through trophic cascades: Linking the frugivorous behaviour and seed dispersal patterns of mesocarnivores

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Abstract

1. Current global change scenarios demand knowledge on how anthropogenic impacts affect ecosystem functioning through changes in food web structure. Frugivorous mesocarnivores are a key link in trophic cascades because, while their abundance and behaviour are usually controlled by apex predators, they can provide high-quality seed-dispersal services to plant communities. Thus, the recent rewilding of large carnivores worldwide can trigger cascading effects for plants.
2. We investigated the top-down effects of an apex predator (Iberian lynx *Lynx pardinus*) on seed-dispersal services mediated by two mesocarnivore species (red fox *Vulpes vulpes* and stone marten *Martes foina*) at the plant community level by comparing areas with and without lynx in a Mediterranean mountain range in Southern Spain.
3. We collected scats of mesocarnivores ($n = 1575$) to assess frugivory and seed dispersal of 15 plant species over two consecutive fruiting seasons and two habitat types (open and forest). Specifically, we assessed the effect of lynx presence on (i) seed occurrence and fleshy-fruit biomass per scat, (ii) number of scats containing seeds and (iii) diversity of dispersed seeds.
4. The quantity and diversity of dispersed seeds drastically decreased under predation risk for both mesocarnivore's species. Seed dispersal by stone martens was negatively affected by the presence of lynx, with a marked reduction in the number of scats with seeds (93%) and the diversity of dispersed seeds (46%). Foxes

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dispersed 68% fewer seeds in open habitats when coexisting with lynx, probably leading to differential contributions to seed-dispersal effectiveness among habitats.

5. Our study reveals a novel trophic cascade from apex predators to plant communities. The behavioural responses of frugivorous mesocarnivores to predation risk and the reduction in the intensity of their faecal deposition pattern are probably related to their lower abundance when co-occurring with apex predators. While rewilding apex predators is a successful conservation tool, attention should be paid to cascading effects across food webs, particularly where frugivore mega-fauna is missing and mesocarnivores provide unique services to plants.

KEYWORDS

DNA-barcoding, endozoochory, frugivory, Iberian lynx, mesopredator release, Order Carnivora, plant–animal mutualism, seed-dispersal service

1 | INTRODUCTION

Interactions between plants and frugivores are of paramount importance in guaranteeing the functioning of most terrestrial ecosystems (Jordano, 2013b). Plants and fruit consumers have developed an efficient mutualism, which does not necessarily require mutual evolutionary adaptations, known as diffuse co-evolution (Herrera, 1995; Valenta & Nevo, 2020). For instance, alterations in habitat structure (e.g. habitat fragmentation; McConkey et al., 2012), frugivore community composition (e.g. defaunation; Donoso et al., 2020) or frugivore behaviour (e.g. dietary shifts; Morales et al., 2013) can alter plant-frugivore mutualism. Consequently, novel seed-disperser interactions can arise and conversely, the loss of key links can lead to functional decay in plant-frugivore networks (Valiente-Banuet et al., 2015). Although studies on the ecological factors shaping plant-frugivore mutualism are increasing (Corlett, 2021; Rey & Alcántara, 2014; Rogers et al., 2021), the current context of global change is demanding more research regarding the oncoming ecosystem alterations that affect key ecological functions, such as seed dispersal by animals.

Mammalian carnivores play an important role as seed dispersers of fleshy-fruited plants, since opportunistic and adaptable medium to large frugivores represent a key ally for native plant communities (Escribano-Avila, 2019; Herrera, 1989). Carnivores can transport many seeds long-distances (González-Varo et al., 2013) and release them under optimum conditions for germination and seedling establishment (Draper et al., 2022; Escribano-Ávila et al., 2013). Most fleshy-fruited plant species often interact with a diverse assemblage of frugivores but the seed dispersal of large-fruited plants imposes physical constraints. This limitation reduces the availability of dispersal partners to a few number of frugivores, among which mammalian mesocarnivores (i.e. subordinate predators) play a relevant role (Escribano-Avila et al., 2018; González-Varo et al., 2015). Mesocarnivores show functionally unique characteristics compared to other specialised frugivores, such as birds, which are usually

derived from dietary preferences (Rumeu et al., 2020), differential movement abilities and habitat use (González-Varo et al., 2013; Jordano et al., 2007). However, few studies have addressed how ecological alterations affecting carnivore communities ultimately cascade (i.e. top-down effects across lower trophic levels) into the seed-dispersal process (Burgos et al., 2022; Ripple, Estes, et al., 2014; Rogers et al., 2021).

Given the global extirpation of large predators, mesocarnivores are an abundant guild in many ecosystems (mesopredator release hypothesis; Crooks & Soulé, 1999; Ripple, Beschta, et al., 2014). However, apex predators not only control mesocarnivore abundance, but also promote a landscape of fear, which is a change in spatial behaviour that varies according to the perceived predation risk (Gaynor et al., 2019). These behavioural alterations can result in different foraging strategies and habitat use. For instance, reducing the use of high-risk habitats (Burgos et al., 2022; Fedriani et al., 2000), or affecting their territorial-marking behaviour and therefore altering their function as seed dispersers (García-Cervigón et al., 2018). The scientific literature has been biased towards the negative ecological effects of mesopredator release, such as increased predation pressure on prey (Brashares et al., 2010). Nevertheless, the promising conservation strategy of restoring threatened apex predators still remains challenging (Prugh & Sivy, 2020; Wolf & Ripple, 2018). Rewilding apex predators in places where they have been lost for a long time can control mesopredator abundance but also trigger trophic cascades (Ripple et al., 2016), altering food web dynamics (Estes et al., 2011), and ecosystem services provided by mesocarnivores, such as seed dispersal (Draper et al., 2022; Tambling et al., 2018).

Altering the abundance and behaviour of key frugivores can affect the quantity (i.e. number of seeds) and quality (i.e. probability of a dispersed seed surviving to become a new reproductive adult) components of seed-dispersal effectiveness (Schupp, 2007; Schupp et al., 2010). For instance, Burgos et al. (2022) found that the presence of an apex predator reduced the fruit consumption of a Mediterranean tree by mesocarnivores, turning them into less efficient frugivores and

potentially reducing the number of seeds dispersed. In the same line, Cancio et al. (2016) showed that a reduction in the use of degraded habitats by a keystone mammalian seed disperser led to the dispersal collapse of a threatened shrub. Thus, behavioural changes in frugivores can alter their territorial marking patterns and the quality of seed deposition sites (i.e. the local environmental conditions a seed experiences after dispersal), which may affect plant recruitment (Beckman & Rogers, 2013). Findings in tropical defaunated ecosystems have shown that predation risk can determine the diversity of frugivores and the plant assemblage dispersed by them (Kurten, 2013).

The recent recovery of the threatened Iberian lynx (*Lynx pardinus*) along the Iberian Peninsula offers a unique opportunity to better understand trophic cascades in a complex and scarcely explored system (Estes et al., 2011). This study aimed to assess the top-down effects of the Iberian lynx on the seed-dispersal patterns of mesocarnivores under a quasi-experimental scenario by comparing areas with lynx presence and lynx-free areas in a Mediterranean forest in Southern Spain. We hypothesised that lynx would alter the seed-dispersal service provided by mesocarnivores at the plant community level. In particular, we expected to observe reduced fruit consumption and faecal marking of mesocarnivores in the presence of lynx. We also predicted that the type of seed-arrival habitat would vary among predation risk scenarios. We expected lower mobilisation of seeds in open vegetation habitats in the presence of lynx because this scenario is more prone to predation risk owing to the scarcity of shelter. At last, we expected that a lower abundance of mesocarnivores would lead to reduced provision of seed-dispersal services in terms of the quantity, quality and diversity. This will lead to varying compositions of plant assemblages dispersed by mesocarnivores among predation risk scenarios, resulting in potentially dissimilar plant communities.

2 | MATERIALS AND METHODS

2.1 | Study area and species

This study was conducted in Sierra de Andújar Natural Park in Southern Spain (Figure 1). The annual average temperature (~18°C) and rainfall (~700mm) of the study area are typical of Mediterranean climate areas (data from Andújar meteorological station, AEMET Open Data Repository, 2020) at altitudes ranging between 400 and 800m. The Natural Park is composed of extensive game lands, where hunting of large wild game ungulates is extensive. Small-game hunting and predator control are infrequent. The vegetation is dominated by Mediterranean shrubland and an arboreal stratum of holm oak (*Quercus ilex*) mixed with a rich community of wild fleshy-fruited species.

This Natural Park provides shelter for one of the largest populations of the Iberian lynx. This threatened apex predator has expanded its distribution range over the last 20 years due to multiple conservation efforts (Simón et al., 2012). However, lynx home ranges are heterogeneously distributed throughout our study area (Figure 1), following the distribution of its main prey, wild rabbits (*Oryctolagus cuniculus*). The Iberian lynx co-occurs with a rich community of

mesopredator species in the study area, including frugivorous carnivores such as red fox (*Vulpes vulpes*), stone marten (*Martes foina*), common genet (*Genetta genetta*) and Eurasian badger (*Meles meles*). Large-fruited plants such as the strawberry tree (*Arbutus unedo*) or the Iberian pear (*Pyrus bourgaeana*) have fruit diameters (more than 10mm; see Herrera, 1984, 1989) larger than the gape width of main European avian seed dispersers, turning mesocarnivores into key seed dispersers. Fruit constitutes up to 60% of the diet of fox and stone marten, despite their generalist dietary nature (Monterroso et al., 2020; Rosalino & Santos-Reis, 2009).

2.2 | Experimental design and scat sampling

We used an experimental design comparing five localities with a year-round territorial presence of reproductive Iberian lynx individuals and five localities without lynx with similar habitat characteristics (Figure 1). Thus, we were able to compare the seed-dispersal patterns of mesocarnivores among predation-risk and predation-free scenarios. We studied the lynx distribution and abundance of mesocarnivores using camera-trapping surveys before carrying out this study (Table S1; Burgos et al., 2023). Since mesocarnivores can alter their habitat-use patterns under predation risk, we selected two different types of habitats in each locality which could affect the environmental conditions of the seed deposition sites and seed-dispersal effectiveness (Schupp, 2007; Schupp et al., 2010): (a) mature forest with a dense shrub stratum and (b) open vegetation with scarce shrubs and isolated trees (see Figure 1; Figure S1). Along 1.5km transects previously selected in each habitat type, we conducted mesocarnivore scat sampling from October to March 2018–2019 and 2019–2020. Transects were existing trails due to the difficulty to walk at random in this mountainous area. This methodology has proven to be efficient for sampling mesocarnivore scats (Martin-Garcia et al., 2022). Sampling was conducted at 1.5-month intervals, allowing each transect to be replicated four times per fruiting season, for a total of 160 visits (four replicates per transect × two habitats × 10 sites × two seasons). Two mammalian scat experts sampled the transects (~3m in width) twice on the same day with a 1-m buffer on both sides of the transect. Most mammalian carnivores deposit their faeces at the border of the main trail, beneath vegetation or on top of conspicuous shrubs or stones; thus, this sampling protocol was effective for finding scats. However, we did not find any scat of common genets because the faecal marking behaviour of this species is often linked to the use of latrines on conspicuous and elevated spots, which would require a different sampling design (Espírito-Santo et al., 2007). Following Putman (1984), experts visually identified scats based on the size, shape, and odour characteristics specific to each carnivore species. In addition, we performed DNA barcoding analysis on a subsample of 70 stone marten scats to confirm our visual identification (see molecular procedures in Appendix S1). We achieved an identification success rate of 95%, which supports our identification expertise. The scats were stored in paper bags and dehydrated at 30°C in a drying oven for 3–4 days

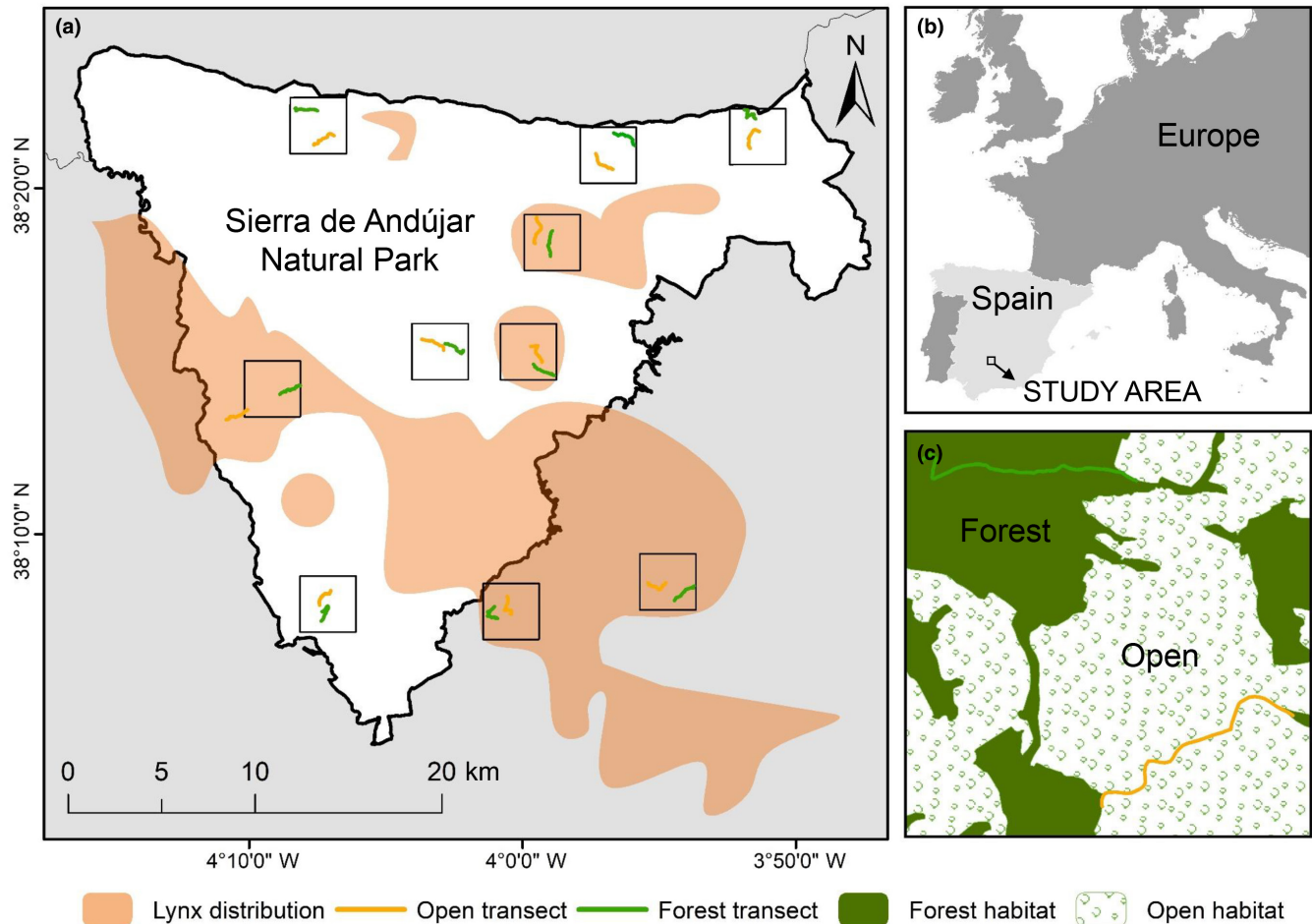


FIGURE 1 (a) Location of the ten study localities where we conducted scat sampling. Orange shadow shows the range of the Iberian lynx (*Lynx pardinus*) along Sierra de Andújar Natural Park adapted from the data available on the IUCN Red List of Threatened Species (Rodríguez & Calzada, 2015). Orange and green routes represent the 1.5-km transects ($n=20$) carried out in open and forest habitats in each locality and fruiting season ($n=160$). (b) Location of the study area in Southern Spain. (c) One of the study locality illustrating the sampling design across open and forest transects. Landscape map produced in ArcGIS v.10.6 by using the National Forest Map 1: 50,000 (MITECO, 2013).

to avoid fungal growth. Fieldwork was approved by the Sierra de Andújar Natural Park, under permit PNSierraAndújar/300/2018 in accordance with animal welfare regulations.

2.3 | Seed content, fruit biomass and seed diversity estimates

We estimated the seed content of the collected faeces to quantify the potential effect of predation risk on quantitative seed dispersal. The dried scats were carefully broken up and the seed content was extracted using decreasing sieve sizes (see photographs in Figure S1). Two experts visually identified the seeds according to morphological concordance with a reference collection (see González-Varo et al., 2021, for a similar approach). The number of seeds in each scat was quantified by counting them under a lens in a Petri dish. When the number of seeds exceeded 100 ($n=24$) within one scat, we divided the seed content into four homogeneous quadrants and extrapolated the number of seeds in one quadrant to the entire sample through multiplication. The fleshy-fruit biomass per scat was estimated to

quantify the effect of lynx on the fruit consumption behaviour of mesocarnivores (we assumed mesocarnivores ate the whole fruit). We used the number of quantified seeds per scat and relationship between the average number of seeds per fruit and the average fleshy-fruit biomass obtained from the *frubase* database (Jordano, 2013a) for each consumed plant species. We then calculated two metrics of alpha seed diversity for each locality and fruiting season to determine the differences in the effective number of equally common and dominant species among predation risk scenarios: (1) Hill-Shannon and (2) Hill-Simpson (Chao et al., 2014; Roswell et al., 2021).

$$\left(e^{-\sum_{i=1}^S p_i \log(p_i)} \right), \quad (1)$$

$$\left(\frac{1}{\sum_{i=1}^S (p_i)^2} \right), \quad (2)$$

where S is plant species richness and p_i is the quantitative contribution to seed rain (i.e. the number of seeds mobilised) of each dispersed plant species in the community. We used our scat-level dataset to estimate

sample coverage and sampling completeness to prove that our results on alpha diversity were not driven by sampling effort (see details in Table S2 and Figures S2 and S3). We followed the rarefaction and extrapolation method proposed by Chao et al. (2014) using the R package iNEXT (Hsieh et al., 2016). We found no significant differences between the predation risk scenarios in either sample coverage ($p=0.11$) or sampling completeness (all $p \geq 0.12$). At last, we determined the beta diversity between predation risk scenarios to determine whether the potential dissimilarity in seed-dispersal diversity was due to species replacement (turnover) or the loss of certain species (nestedness) using the R package betapart v.1.5.6. (Jaccard's index; Baselga, 2010).

2.4 | Fruit density and diversity estimates

To account for the potential effects of fruit availability on fruit consumption and seed dispersal by mesocarnivores, we estimated the available fruit density during the fruiting peak. At the same time that we carried out scat sampling, we visually estimated the coverage percentage and the individual crop size inside plots of 15 × 15 m every 200 m on both sides of each transect. We estimated crop size using a semi-logarithmic fruit abundance index: 0 = no fruits, 1 = 1–10 fruits, 2 = 11–100 fruits, 3 = 101–1000 fruits, 4 = 1001–10,000, 5 > 10,000. Fruit estimation was performed only along forest habitat-type transects because, in open habitats, fleshy-fruited plants were rare or absent, except for *P. bourgaeana*. This tree most often occurred on substrates lacking other vegetation. Therefore, we estimated its crop size by searching for adult individuals in a 100 m buffer across the open habitat transects. Peak fruit density (no. fruits/m²) for each plant species was calculated for each locality and fruiting season as the average crop size of all sampled plots along each transect. Fruit diversity was calculated as the Hill-Shannon/Simpson diversity index of available fruits to describe seed diversity.

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Study locality	Study locality	5 localities with lynx and 5 localities without lynx each study year (×2)
Study locality	Habitat type	2 transects per locality, 1 in forest and 1 in open habitat, totalling 10 transects per habitat type each study year (×2)
Species	Mesocarnivore's scat	175 scats of stone marten and 1400 scats of red fox

2.6 | Statistical analyses

We fitted generalised and linear mixed models using the R package lme4 v.1.1-27.1 (Bates et al., 2020) to evaluate the effects of Iberian lynx presence, habitat type, and fruit availability on fruit consumption and seed-dispersal patterns of mesocarnivores. We also fitted generalised linear models to assess the effects of lynx presence on seed-dispersal diversity by mesocarnivores. Pearson correlation test was performed between the number of scats and the number of seeds dispersed by carnivores to determine the relationship between scent marking and seed-dispersal patterns between predation risk scenarios.

2.7 | Response variables

We modelled red fox and stone marten data separately for fruit consumption and seed dispersal and analysed the following response variables: (1) seed occurrence per scat (Bernoulli-distributed variable: 0 = absence, 1 = presence), (2) fleshy-fruit biomass per scat (zero not included), (3) number of scats with seeds (zero included) and (4) seed diversity. As badger scats were scarce ($n=26$) and only found outside lynx territories, this species was not considered in our analysis. We chose fruit biomass and the number of scats with seeds as response variables as unbiased measures of fruit consumption of the whole plant community, given that fruits and seeds consumed are influenced by fruit size and seed content of each plant species, respectively. Seeds of common fig and rare plant species (grouped in 'Others') were not included in the modelling because of their low occurrence in carnivore diets (see Figure 2) but were included in the diversity analyses. We used binomial errors for seed occurrence, Gaussian errors (identity link) on log-transformed data for fruit biomass, Poisson errors (log link) for the number of scats with seeds and gamma errors (log link) for seed diversity.

2.8 | Fixed and random effects

We used lynx presence or absence (L) as fixed effect. Fruit density (FD; no. fruits/m²) was included as fixed effect for seed occurrence, fruit biomass and scats with seeds models. Fruit diversity was previously discarded because it resulted in non-significant Pearson's correlations with seed diversity (Figure S4) to avoid overfitting owing to the reduced sample size ($n=20$). We also added habitat type (H) to the number of scats with seeds as a fixed term. Interactions FD × L and H × L were also included in the respective models to account for the differential effects of these variables among the predation risk scenarios. Fruiting season ($n=2$) was also added as fixed effect for all response variables. Locality ($n=10$) was added as random effect in all mixed models, except for the seed diversity models.

2.9 | Model selection

Candidate models contained all the possible combinations with a biological sense of fixed effects and interaction terms explained above, compared to models without our variable of interest, lynx presence/absence and a null model (intercept). Due to the reduced sample size for seed diversity, we performed model selection by comparing models including only the fixed term lynx (L) with null models. We ranked the candidate models according to Akaike information criterion adjusted for small sample sizes (AICc). If no other models were within two AICc units from the top ranked model ($\Delta\text{AICc}=0$), the top model was considered the best but if other models were within two AICc units of the top model ($\Delta\text{AICc} \leq 2.0$) these were considered to be a set of models with similar support (Burnham & Anderson, 2002). We used the MuMIn package v.1.43.17 (Barton, 2013) for model selection. We calculated the marginal and conditional coefficients of determination (pseudo- R^2) for the selected models (Nakagawa et al., 2017). We carried out post-hoc simple-slope pairwise comparisons to estimate the model coefficients of the interaction terms using the R package emmeans v.1.6.3 (Russell V et al., 2021). Model residuals were inspected using the DHARMA package v. 0.4.6 (Hartig & Lohse, 2022) and a Moran's I test indicated no spatial autocorrelation (p -values > 0.05 ; see Figure S5). All analyses were conducted in R (version 3.6.1; R Core Team, 2019).

3 | RESULTS

3.1 | General overview

We collected 1575 scats from two mesocarnivorous species: red fox ($n=1400$) and stone marten ($n=175$). Of these, 64% and 91% were collected outside lynx territories, respectively, and 49% and 74% contained seeds. The red fox dispersed a total of 30,070 seeds and the stone marten 3972, with 63% and 88% dispersed outside lynx territories respectively. We found a positive correlation between the number of scats and seeds dispersed, except for stone marten in the

presence of lynx, which was probably due to the small sample size (Figure S6).

Mesocarnivores dispersed up to 15 fleshy-fruited plant species. The most consumed fruit was *A. unedo*, which appeared in 67% of scats with seeds, followed by *P. bourgaeana*, *J. oxycedrus*, *R. ulmifolius*, *M. communis*, *O. europaea* and *F. carica* (Figure 2). Other small-sized plant species were found at very low percentages (less than 1%). The most abundant fleshy-fruit along transects was *O. europaea*, followed by *J. oxycedrus* and *A. unedo*, whereas *P. bourgaeana* was the scarcest (Figure S7A). Fruit density, Hill-Shannon and Hill-Simpson diversity of the wide community of fleshy-fruited plants did not significantly differ between the predation risk scenarios ($F=2.18$, $p=0.17$; $F=1.28$, $p=0.27$; and $F=1.08$, $p=0.31$, respectively; Figure S7B).

3.2 | Seed occurrence and fleshy-fruit biomass

The occurrence of seeds in scats of red fox and stone marten was 1.2 and 1.4 times higher outside than inside lynx territories, respectively (Figure S8). For the red fox, the top model contained lynx, fruit density and their interaction (Table S3). Under both predation risk scenarios, the relationship between seed occurrence and fruit density was positive (see Table S4) but there was significantly lower seed occurrence in scats under predation compared to predation free scenario (Figure S9E,F) (Coeff. \pm SE: -0.10 ± 0.11 in lynx presence vs. 0.27 ± 0.10 in lynx absence). For the stone marten, fruit density was included in the top model set (Table S3) with a negative effect on seed occurrence (Table S4).

Lynx occurrence did not show any effect on the fleshy fruit biomass in red fox scats (Table S3). However, lynx had a significant effect on fruit biomass per stone marten scat, which was on average 2.4 times higher inside than outside lynx territories (Table S3). This strong effect was mainly driven by *A. unedo* (Figure 3). Fruit density was included in the best models only for stone marten (Table S3) with a significant and negative effect on fruit biomass per scat (Table S4).

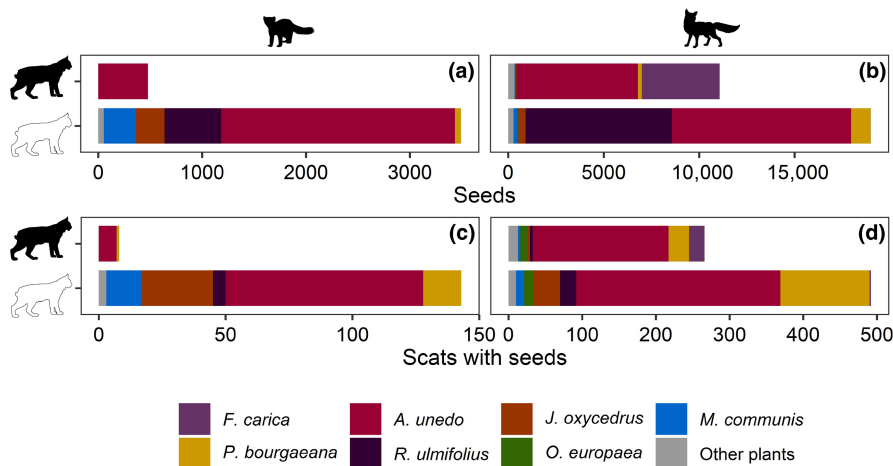


FIGURE 2 Additive number of seeds dispersed by stone marten (a) and red fox (b) and scats of stone marten (c) and red fox (d) with seeds in sites with Iberian lynx presence (coloured lynx silhouette) and absence (non-coloured lynx silhouette). Since a scat can contain multiple plant species, the total number of scats with seeds (c, d) shows the addition of scats with different plants species. The total number of scats with seeds was 239 and 8 under lynx presence and 452 and 121 under lynx absence, for red fox and stone marten respectively.

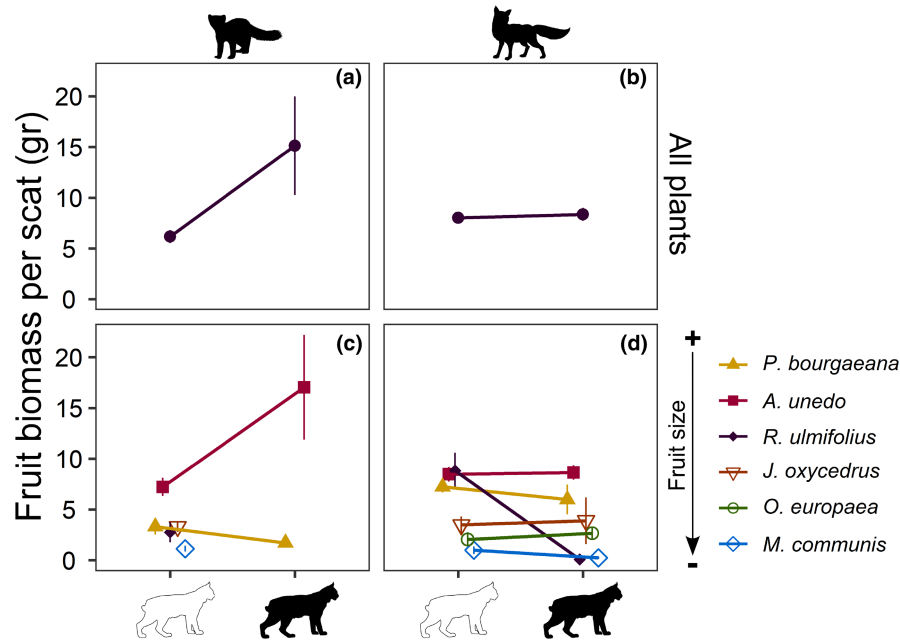


FIGURE 3 Average estimated fleshy-fruit biomass (gr) of all plants consumed per scat with seeds of (a) stone marten ($n=127$) and (b) red fox ($n=661$) and each plant species separately (c, d) in sites with presence of Iberian lynx (coloured lynx silhouette) and absence of lynx (non-coloured lynx silhouette). Bars represent standard errors and lines show the trend between predation risk scenarios. Fruit biomass was calculated by using the number of quantified seeds per scat and the relationship between the average number of seeds per fruit and the average fleshy-fruit biomass obtained from the *frubase* database (Jordano, 2013a). Plant species are represented by different colours. Arrow shows the decreasing variation in fruit size. All plants refer to the additive fruit biomass per scat of all plant species.

3.3 | Seed dispersal and seed-deposition habitat

The best models for the number of stone marten scats with seeds included lynx occurrence and habitat type (Table S3). Stone marten dispersed a significantly lower proportion of seeds (93% lower) in lynx presence than in lynx absence scenarios (Figure 2). The proportion of scats with seeds was higher in forest habitats compared to open habitats (up to six times) regardless of the predation risk scenario (Table S3; Figure 4a). The best models for the red fox included the interaction between habitat and lynx (Table S3). Red fox deposited 0.5 times fewer scats with seeds in open habitats (Coeff. \pm SE: 1.91 ± 0.19) than in forest habitats (2.70 ± 0.17) inside lynx territories (Figure 4b). The proportion of scats with seeds was similar between habitats under lynx absence (53% vs. 47%) (Figure 4b). The interaction between lynx presence and fruit density was included in the best models for the red fox. We found fruit density created a contrasting pattern on the number of scats with seeds between the predation risk scenarios, with a significant positive effect of fruit density under lynx absence while under the presence of lynx the relationship had a negative trend (Figure S9A–D).

3.4 | Alpha and beta diversity of dispersed seeds

Lynx presence reduced the diversity of common (Hill-Shannon) and dominant (Hill-Simpson) plant species dispersed by

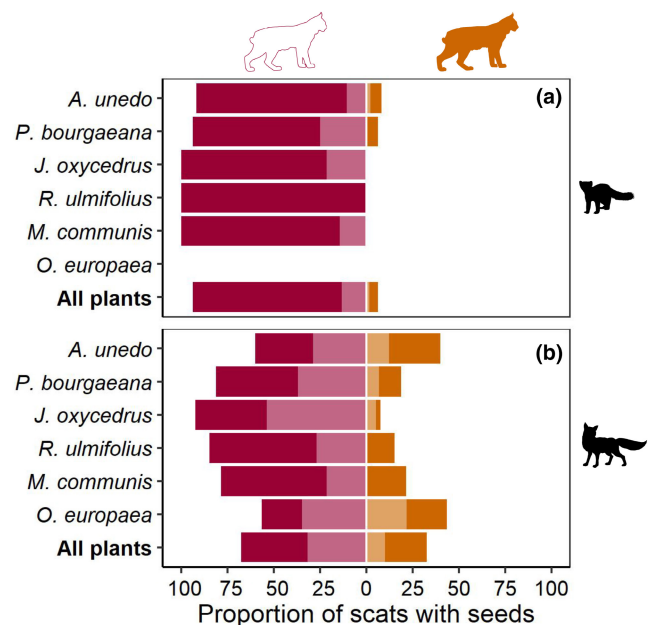


FIGURE 4 Proportion of scats with seeds of (a) stone marten and (b) red fox deposited in sites with presence of Iberian lynx (orange colour) and sites without lynx (magenta colour) for each plant species. Dark orange and dark magenta refer to forest habitat type and light orange and light magenta to open habitats. Values increase to the left on the plot for localities without lynx, and the opposite for the plot with lynx presence. All plants refer to the proportion of scats with seeds of any plant species.

mesocarnivores (Tables S5 and S6). Hill-Simpson was significantly lower in the presence of lynx in seeds dispersed by stone martens but not in those dispersed by red foxes (Table S5). Red fox and stone marten mobilised a similar average diversity of seeds outside lynx territories but inside lynx territories, red fox dispersed a higher seed diversity than stone marten (Figure 5a,b) for both common and dominant species (1.5 and 1.4 times higher, respectively). Finally, we found higher dissimilarity of plant species dispersed by stone marten than red fox (mean Jaccard's=0.73 and 0.29, respectively) between predation risk scenarios (Figure 5e). Beta diversity was completely driven by the loss of species (nestedness) for stone marten; however, for red fox, the contribution varied between species replacement (turnover) and loss (nestedness) in each fruiting season (Figure 5c,d).

4 | DISCUSSION

Our results showed that the seed-dispersal patterns of mesocarnivores in a Mediterranean fleshy-fruited plant community were altered

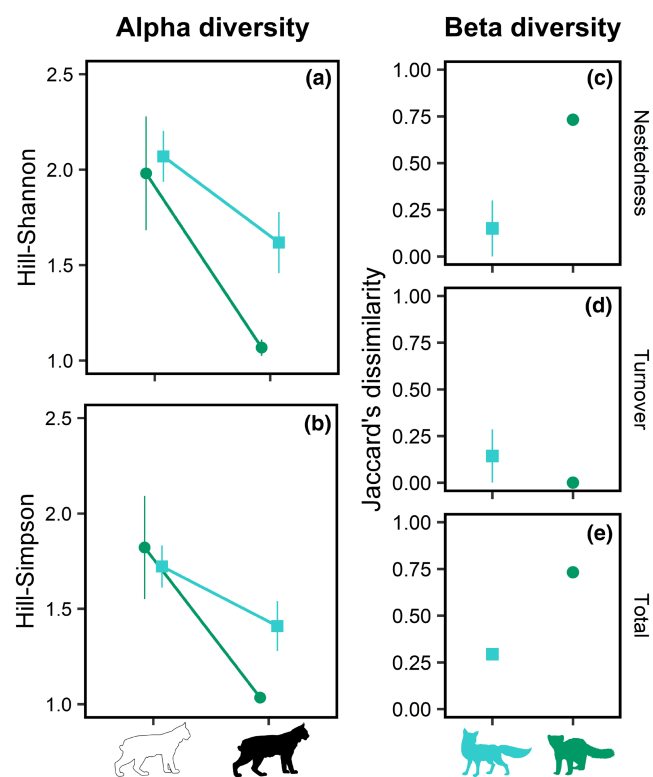


FIGURE 5 Alpha and Beta diversity of dispersed plant species for red fox (blue) and stone marten (green). Alpha diversity is shown in terms of Hill-Shannon (a) and Hill-Simpson (b) indices and was estimated at level of locality and fruiting season. Beta diversity between predation risk scenarios of each fruiting season is expressed in terms of Jaccard's (e) and its components: nestedness (c) and turnover (d). Circles represent observed average values with their correspondent standard errors (bars). Coloured lynx silhouette denotes presence of Iberian lynx and non-coloured silhouette denotes sites without lynx.

by the presence of an apex predator. The Iberian lynx modified the frugivory and faecal-marking behaviour of mesocarnivores, what potentially would trigger a trophic cascade down to plants. Apex predators can reduce mesocarnivore abundance (Newsome et al., 2017) and alter their behaviour (Ritchie & Johnson, 2009) via top-down effects. The resultant combined effect leads to reduce seed dispersal by mesocarnivores and to promote differing assemblages of dispersed seeds between predation risk scenarios, with unforeseen consequences for plant establishment. Although the mutualistic interaction between frugivorous carnivores and fleshy-fruited plants can be altered in apex predator rewilding scenarios, this returns seed dispersal by mesocarnivores to a more natural state before lynx eradication.

4.1 | Frugivory behaviour and seed dispersal in a landscape of fear

Frugivorous mesocarnivores are frequently suppressed by larger predators which search for and kill competitors, as is the case with the Iberian lynx (Jiménez et al., 2019; Palomares & Delibes, 1994). This top-down effect constrains mesocarnivore abundance and leads to reduced seed dispersal in areas inhabited by lynx. Predation risk can also alter the foraging behaviour of frugivores or even reduce the visitation rate of fruiting trees in risky areas, both via top-down suppression and behavioural alterations (Burgos et al., 2022; Carreira et al., 2020; Selwyn et al., 2020). Although the fleshy fruit biomass of certain preferred and abundant fruits can be greater under predation risk (see *A. unedo* in Figure 3), there was a global reduction in the quantitative component of seed mobilisation, probably driven by the lower abundance of frugivorous carnivores. Faecal scent-marking is a territorial behaviour that evolves into inter-individual communication (Gorman & Trowbridge, 1989); therefore, fewer animals leads to fewer faecal marks and seed-dispersal events. Consistent with our findings, previous studies have found that simplification of the frugivore community can lead to a decay in dispersal function, either by rearranging plant-frugivore interactions, altering interaction strength or a combination of both (Rogers et al., 2021).

In addition to its quantitative effect on seed rain, the presence of an apex predator can alter the quality of the seed dispersal. In the presence of lynx, red fox reduced faecal-marking in open habitats, probably as a consequence of a behavioural adaptation to avoid intra-guild competition in risk-exposed areas (Ferreiro-Arias et al., 2021; Schmitz et al., 1997). This adaptable marking behaviour of red fox translates into shifts in seed-arrival patterns (García-Cervigón et al., 2018), with proportionally fewer seeds being deposited in open environments. Habitat suitability is a qualitative component of seed-dispersal effectiveness (Schupp, 2007) that impacts the probability of seedling recruitment and thereby influences the quality of dispersal services (Beckman & Rogers, 2013; González-Castro et al., 2015). In Mediterranean ecosystems, where the shortage of water supply and high herbivory severely limit plant recruitment (Mendoza et al., 2009; Perea et al., 2020), landing in forest habitats can positively affect seedling emergence, survival, and ultimately plant spatial distribution

(Fedriani et al., 2018; Fedriani & Delibes, 2009). Lynx presence may limit the colonisation of certain plant species towards open habitats, affecting plant-community structure (such as the Iberian pear; see Figure 4) and the colonisation potential in response to global change (Schleuning et al., 2020). Nevertheless, at the same time apex predators can contribute to maintaining the valuable 'mosaic landscapes' by biasing seed dispersal towards forests (Brotons et al., 2018; Curveira-Santos et al., 2017).

4.2 | Loss of the seed-dispersal service provided by stone marten

Contrary to the distinctive spatial pattern shown by red fox, stone marten did not modify the seed-arrival habitat in the presence of the apex predator, probably because it is a forest-dwelling species (Virgós et al., 2020). Stone marten barely dispersed seeds in the presence of the Iberian lynx, probably as a result of its low abundance. This result agrees with its strong avoidance to large predators (Monterroso et al., 2020; Virgós et al., 2020) and its severe abundance decrease in response to predation risk (Jiménez et al., 2019; see Table S1). In addition, stone marten almost exclusively fed on *A. unedo* fruits under predation risk. This is a sugar-rich fruit (Herrera, 1987) and highly abundant in this landscape of fear, which would support this preference (López-Bao & González-Varo, 2011; Virgós et al., 2010). These findings suggest a possible dietary specialisation towards the preferred food resource as a result of a cost-benefit balance (Brown & Morgan, 1995), similar to Gazzola and Balestrieri (2020) found in an intraguild competition scenario of two marten species.

Specific threats affecting keystone seed dispersers, such as stone marten, can lead to the rapid collapse of community-level dispersal services in the absence of alternative frugivores (Rumeu et al., 2017). The marked functional diversity of carnivores and their low functional redundancy with other groups of frugivores, such as birds (Nakashima & Do Linh San, 2022; Rumeu et al., 2020) make each species unique in terms of seed dispersal services. Furthermore, although migratory birds are important drivers of long-distance seed dispersal (González-Varo et al., 2021), seed rain is frequently restricted to the parental plant surroundings (Jordano et al., 2007). Escribano-Ávila et al. (2014) found that martens and foxes played a key role in land abandonment colonisation processes for *Juniperus thurifera* by dispersing seeds far from the adult plants. This contribution to seed flow among contrasting habitat types is highly valuable in disturbed landscapes, whereas frugivorous birds frequently avoid open habitats lacking tree vegetation cover (García et al., 2010; González-Varo et al., 2023).

4.3 | Trophic cascades affect the diversity of dispersed seeds

A larger array of frugivores can promote the consumption and mobilisation of a more diverse ensemble of fruiting plants, probably

driven by functional complementarity (García et al., 2018; García-Rodríguez et al., 2022), as found under lynx absence. However, in lynx presence seed diversity decreases because of a trophic cascade, as previously defaunated ecosystems has shown (Kurten, 2013). Diversity reduction was controlled by two community structuring mechanisms: nestedness and turnover. Nestedness was explained by the loss of species dispersed by stone marten (*M. communis* or *J. oxycedrus*). However, some fruits dispersed by fox outside lynx territories were replaced by other species in sites with lynx (turnover), leading to a more balanced variation in beta diversity among predation risk scenarios (e.g. *F. carica* and *R. ulmifolius*; see Figure 2b).

4.4 | Impact of trophic cascades on large-fruited plants

The largest and favourite fruit species (*A. unedo* and *P. bourgaeana*) may be the most affected by this trophic cascade, because they usually depend on the seed-dispersal service provided by large frugivores (Escribano-Ávila et al., 2013; Fedriani & Delibes, 2009). This type of large fruits, often have high pulp-to-seed ratios (Fedriani & Delibes, 2009), which leads to low quantitative seed dispersal even in the absence of predation risk (see Figure 2). However, the presence of an apex predator may limit the availability of seeds for recruitment, constraining regeneration dynamics (Rogers et al., 2021) and old-field colonisation processes where mesocarnivores play key roles (Escribano-Ávila et al., 2014; Fedriani et al., 2018). This may be particularly relevant in ecosystems where larger frugivores (i.e. megafauna) are extinct. This is the case of Mediterranean ecosystems where the extinct brown bear (*Ursus arctos*) likely played a key role in seed dispersal for large-fruited plant species. However, other large- and medium-sized frugivores whose abundance and behaviour are not affected by the presence of lynx (e.g. badgers) could compensate for the lost seed-dispersal functions (Fedriani et al., 2020; García-Rodríguez et al., 2022; Vidal et al., 2013). Hence, understanding the cascading effects of rewilding apex predators could be particularly relevant in defaunated ecosystems, where mesocarnivores maintain key mutualism with fleshy-fruited plants.

5 | CONCLUSIONS

The present study supports our hypothesis that, in an apex predator rewilding scenario, the fleshy-fruited plant community experiences a drastic decrease in the diversity and quantity of seeds dispersed, with potential consequences for the recruitment patterns of the whole plant community. Trophic cascades are powerful mechanisms, which can affect the processes that drive seed dispersal. These complex community effects should be considered when planning future large predator reintroductions, particularly in defaunated ecosystems lacking frugivorous megafauna.

AUTHOR CONTRIBUTIONS

TB, GE-A, JMF and EV conceived the idea, methodology and the manuscript approach; TB, JH-H and IC collected the data; TB, JPG-V and JCI carried out the DNA barcoding analyses; TB analysed the data; TB led the writing. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b2rbnzsp> (Burgos et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Molecular procedures.

Appendix S2: Tables.

Appendix S3: Figures.

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