OIKOS

*Research Article*

# Frugivory-mediated trophic cascades: how apex predators can shape the recruitment of a fleshy-fruited tree

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**Oikos**
**2026: e11524**
doi: 10.1002/oik.11524
Subject Editor: Kim McConkey
Editor-in-Chief: Pedro Peres-Neto
Accepted 2 October 2025

The recovery of large carnivores offers unique opportunities to study their cascading impacts on plant population dynamics. Medium-sized carnivores, both prey and seed dispersers, are suppressed by apex predators, indirectly increasing seed-eating rodent's populations and potentially altering plant establishment. We investigated how natural variation in the presence of the Iberian lynx *Lynx pardinus*, a top predator in southern Spain, triggered cascading effects on the recruitment of the Iberian pear *Pyrus bourgaeana* through altered seed dispersal patterns by mesopredators and post-dispersal seed predation by rodents. To assess whether and how the seed-dispersal effectiveness of the Iberian pear was influenced by lynx presence across different habitats (open, forest) and microsites (shrub, rock and open), we conducted field experiments and observations spanning multiple life-cycle stages of this fleshy-fruited tree mainly dispersed by carnivorous mammals. Path analysis revealed that lynx presence decreased seed dispersal by 80% and biased it toward forests, where seedling survival was extremely low (1%). Most of the seeds were delivered in open microsites (61%), particularly in lynx absence by the red fox. Although we detected no direct effect of lynx presence on post-dispersal seed predation, rodents removed 49 and 116% more seeds under shrubs than in rock and open interspaces, respectively, negatively affecting plant recruitment. Since shrubs provided the most favourable conditions for seedling survival, particularly in open habitats, these results expose a seed-seedling conflict, whereby microsites with the highest seed predation are also those that maximize seedling establishment. This may limit the expansion potential of the Iberian pear and likely other fleshy-fruited species given the current global rewilding context. Reintroduction programs of threatened carnivores should account for trophic cascades that may disrupt frugivory interactions and ultimately shape plant recruitment and establishment. This is especially relevant in defaunated ecosystems, where plant–animal mutualisms are often compromised.

Keywords: defaunation, mesopredators, multi-trophic interactions, post-dispersal seed predation, predation risk, seed-dispersal effectiveness

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## Introduction

Trophic cascades are powerful mechanisms structuring ecosystems across food webs (Terborgh et al. 2010, Estes et al. 2011, Ripple et al. 2016). Top–down effects often ripple through successive trophic levels, from apex predators to primary producers, affecting plant communities and entire ecosystem dynamics (Ripple and Beschta 2005, Choquenot and Forsyth 2013). Plant–animal mutualistic interactions, such as pollination and seed dispersal, can be altered by these cascades, often as a result of human impacts. For instance, frugivore loss in defaunated ecosystems has been shown to affect plant seed dispersal (Cordeiro and Howe 2003, Wotton and Kelly 2011, Traveset et al. 2012, Fedriani et al. 2020a), compromising the stability and dynamic of many plant populations. However, much less is known about whether the reintroduction or recovery of apex predators can influence the recruitment and establishment of plants via trophic cascades affecting frugivory interactions. This is especially important because many fleshy-fruited plants have lost some of their legitimate seed dispersers (Vidal et al. 2013, Malhi et al. 2016, González-Varo 2024), making it essential to assess the consequences of apex predator recovery in the context of global rewilding efforts.

Populations of large carnivores are recovering worldwide as a result of targeted conservation actions, including both active rewilding (i.e. reintroductions) and passive rewilding through natural recovery following threat mitigation (Wolf and Ripple 2018). The recovery of apex predators can trigger trophic cascades that influence lower trophic levels, including mesopredators, which may be displaced to less productive areas due to increased predation risk (Brown et al. 1999, Gallagher et al. 2017, Burgos et al. 2023). The recovery of apex predators creates a 'landscape of fear,' where behaviourally-mediated trophic cascades affect subordinate predators' habitat use and foraging behaviour (Schmitz et al. 1997, Pasanen-Mortensen et al. 2013, Burgos et al. 2022). Apex predators may also directly suppress mesopredator populations through intra-guild predation, leading to potential cascades in ecosystem functions (Linnell and Strand 2000, Brashares et al. 2010, Tambling et al. 2018).

Some mammalian carnivores play a key role as seed dispersers for many fleshy-fruit plants (Herrera 1989, Rosalino and Santos-Reis 2009), providing a crucial ecosystem service, particularly for plant species that have lost their legitimate seed dispersers (Escribano-Ávila 2019, Cui et al. 2023, Fedriani et al. 2024). However, behavioural changes in frugivorous mesopredators due to apex predator recovery could alter the quantity and quality of seed dispersal, ultimately influencing both the number of dispersed seeds and the probability of seeds developing into adult plants, a process captured by the seed-dispersal effectiveness concept (Schupp et al. 2010). Mesopredators may shift their habitat and microsite preferences in response to predation risk, strongly altering seed deposition patterns (Schupp 2007, Beckman and Rogers 2013, Burgos et al. 2024). In consequence, the displacement of seed disperser activity to safer areas could affect plant recruitment and establishment in contrasting ways (García et al. 2005). If seeds are redirected to highly favourable habitats and microsites, increased recruitment rates might partially or fully compensate for the decline in seed dispersal caused by mesopredator suppression. Conversely, if seeds are deposited in unsuitable sites, these behavioural shifts could exacerbate seed dispersal limitation, ultimately hindering plant establishment.

The top–down effects of apex predators on plant recruitment and establishment remain largely unexplored (Meserve et al. 2003, Ripple and Beschta 2003, Maron and Pearson 2011). Even less is known about how apex predator recovery affects seed dispersal by frugivorous carnivores and the subsequent stages of plant demography. In the Mediterranean ecosystem studied here, the Iberian lynx *Lynx pardinus* acts as an apex predator, reducing the mesopredator populations and indirectly increasing seed-eating rodent abundance (Burgos et al. 2023). The suppression and control of frugivorous mesopredators reduces fruit consumption and seed dispersal, and also modifies the relative availability and spatial distribution of seeds across the landscape of fear (Burgos et al. 2022, 2024). However, it remains unclear how these predator-driven shifts in animal behaviour and seed fate ultimately translate into changes in plant recruitment and establishment patterns across the regeneration cycle.

To evaluate how apex predators indirectly influences plant recruitment, we combined field observations and experiments across several life-cycle stages of a carnivore-dispersed tree, the Iberian pear *Pyrus bourgaeana*, with path analyses. Unlike previous work that focused exclusively on the cascading effects of lynx presence on fruit consumption and quantitative seed dispersal (Burgos et al. 2022, 2024), here we incorporate several aspects of the qualitative component of seed-dispersal effectiveness, including post-dispersal seed predation, seedling emergence and seedling survival across different habitats and microsites. Our goal was to determine how the presence of lynx influences each stage of the early plant recruitment process and identify which demographic transitions most limit successful establishment. We hypothesize that lynx presence, by reducing frugivorous carnivores and increasing seed-eating rodent abundances, will lead to fewer seeds dispersed, reduced post-dispersal seed survival, and ultimately lower seedling emergence and survival. However, we expect that the environmental conditions of habitats and microsites where seeds arrive will critically shape the success of the final recruitment stages, acting as a key ecological filter. Specifically, we predict that the harsh environmental conditions of Mediterranean landscapes (water-stress, exposure, high radiation etc.), especially in open habitats (Mendoza et al. 2009, Perea et al. 2020, Muñoz-Gómez et al. 2024), will limit seedling emergence and survival regardless of lynx presence.

## Material and methods

### Study area

This study was conducted in the Sierra de Andújar Natural Park (SANP), southern Spain (38°14'27.71"N, 04°04'45.03"W,

covering nearly 740 km$^2$; Supporting information). The area experiences a mild annual average temperature (~18°C) and low rainfall (~700 mm), typical of Mediterranean climates (AEMET Opendata 2020). The altitude ranges from 400 to 800 m a.s.l. SANP comprises extensive game lands where large ungulate hunting is common, but predator control is minimal or absent. Mediterranean shrubland predominates, with frequent pine plantations. The key habitat is mature, high-cover forest with a canopy of holm oak *Quercus ilex*, interspersed with species like strawberry tree *Arbutus unedo* and aromatic shrubs (e.g. *Rosmarinus officinalis*). Forests often form a mosaic with open landscapes featuring sparse scrubland and isolated trees such as the Iberian pear.

SANP hosts one of the largest wild populations of the Iberian lynx that has recovered from near-extinction in the 1990s without the need for reintroductions. At that time, fewer than 50 individuals remained in the area, but thanks to targeted conservation actions – such as habitat management and the recovery of key prey like wild rabbits – the population has increased to over 268 individuals (MITECO 2023). Despite this recovery, the lynx's distribution within SANP remains patchy (Supporting information). The lynx coexists with a diverse community of medium-sized predators, including frugivorous species such as the red fox *Vulpes vulpes* and stone marten *Martes foina*. The lynx exerts top–down control by regulating mesopredator populations (except the Eurasian badger *Meles meles*) and altering their foraging behaviour (Burgos et al. 2022, 2023). Fruits are a crucial seasonal resource for frugivorous mesopredators (Rosalino and Santos-Reis 2009), especially when more energy-rich foods like small mammals are scarce (Padial et al. 2002, Bakaloudis et al. 2012). The most common small mammals in SANP are wild rabbits *Oryctolagus cuniculus* and rodents such as the garden dormouse *Eliomys quercinus* and wood mouse *Apodemus sylvaticus*. These species are both seed predators and pulp feeders of several fleshy-fruited plants, including the Iberian pear (Rey et al. 2002, Fedriani and Delibes 2013).

### Study tree species

The Iberian pear is a Mediterranean tree that produces fleshy pomes, rich in sugar and water, with a diameter of 2–3 cm and an average wet weight of ~9.5 g (Fedriani and Delibes 2009a). Its fruits provide a predictable food resource from September to December, peaking in November (Fedriani and Delibes 2009b). Each reproductive tree yields between 100 and over 1000 fruits, each containing 1–5 viable seeds with thin, easily breakable coats. Pre-dispersal seed loss to invertebrates is typically low (Fedriani and Delibes 2009b). In SANP, the Iberian pear occurs at very low densities, even lower than in other Mediterranean regions such as Doñana, with less than one individual per hectare (Fedriani et al. 2010, Morera et al. 2025). It is relatively isolated from other fruiting species, growing in open-vegetation landscapes. This tree exhibits an aggregated spatial pattern, likely due to seed dispersal and seedling clustering, primarily facilitated by the red fox and Eurasian badger, its main seed dispersers (Fedriani and Delibes 2009a, Fedriani et al. 2010). Other frugivores, such as wild boar and some frugivorous birds, occasionally disperse Iberian pear seeds but are largely seed predators or pulp feeders (Fedriani et al. 2012, 2024). Rodents are the main seed predators for this tree species (up to 94.3% of seeds predated; Fedriani and Delibes 2009b). The frequent presence of seed shells of Iberian pear in experimental seed depots indicates that rodents act as seed predators, and no evidence of seed caching by rodents has been found in this system (Fedriani and Delibes 2009b, Enders and Vander Wall 2012). However, scatter-hoarding rodents can also act as 'rescuers' of seeds from aborted fruits of Iberian pear, potentially contributing to secondary seed dispersal (Fedriani et al. 2020b). Most Iberian pear seedlings emerge between late February and late April, with the first summer being the period of highest seedling mortality due to severe droughts typical of Mediterranean climates (Fedriani and Delibes 2009b).

### Seed dispersal in areas with and without lynx

To assess the impact of lynx presence on the Iberian pear seed dispersal, we used the seed dispersal data of this species from Burgos et al. (2024). This dataset provided us a key starting point for understanding how apex predators influence the quantity of seed dispersal. Burgos et al. (2024) assessed seed dispersal by frugivorous mesopredators for the whole fleshy-fruited plant community in five localities with permanent territorial presence of Iberian lynxes and five control localities without lynxes in SANP (Supporting information). Mesopredators were up to 10 times scarcer in areas inhabited by lynx (Burgos et al. 2023, Supporting information). The study localities contained fruiting Iberian pear trees, averaging 0.86 and 1.73 trees per km$^2$ in areas without and with lynxes, respectively. Fruit density (fruits m$^{-2}$) of fleshy-fruited plants estimated along the surveyed transects during the fruiting season did not significantly differ between predation risk scenarios ($F = 2.18$, $p = 0.17$). Burgos et al. (2024) measured seed dispersal in two distinct habitat types: 1) mature forest with a dense shrub layer, and 2) open landscapes with sparse shrub cover and isolated or small clumps of trees (Fig. 1). Mesopredator scat sampling was carried out by two mammal scat experts along 1.5 km × 3 m transects in each habitat type during two consecutive fruiting seasons, from October to March of 2018–2019 and 2019–2020 (Supporting information for details). While Burgos et al. (2024) focused on quantifying seed dispersal by habitat type and lynx scenario, here we build upon it by incorporating the microsite of seed deposition given its importance for plant recruitment (Schupp 1993, Escribano-Ávila et al. 2014). We further differentiated among three microsites of scat deposition: 1) beneath or on a small rock (rock), 2) beneath or on a shrub (shrub), and 3) at open ground (open).

### Post-dispersal seed predation in areas with and without lynx

To examine whether lynx presence indirectly affects seed survival through changes in rodent-mediated seed predation, we conducted a field experiment simulating natural seed

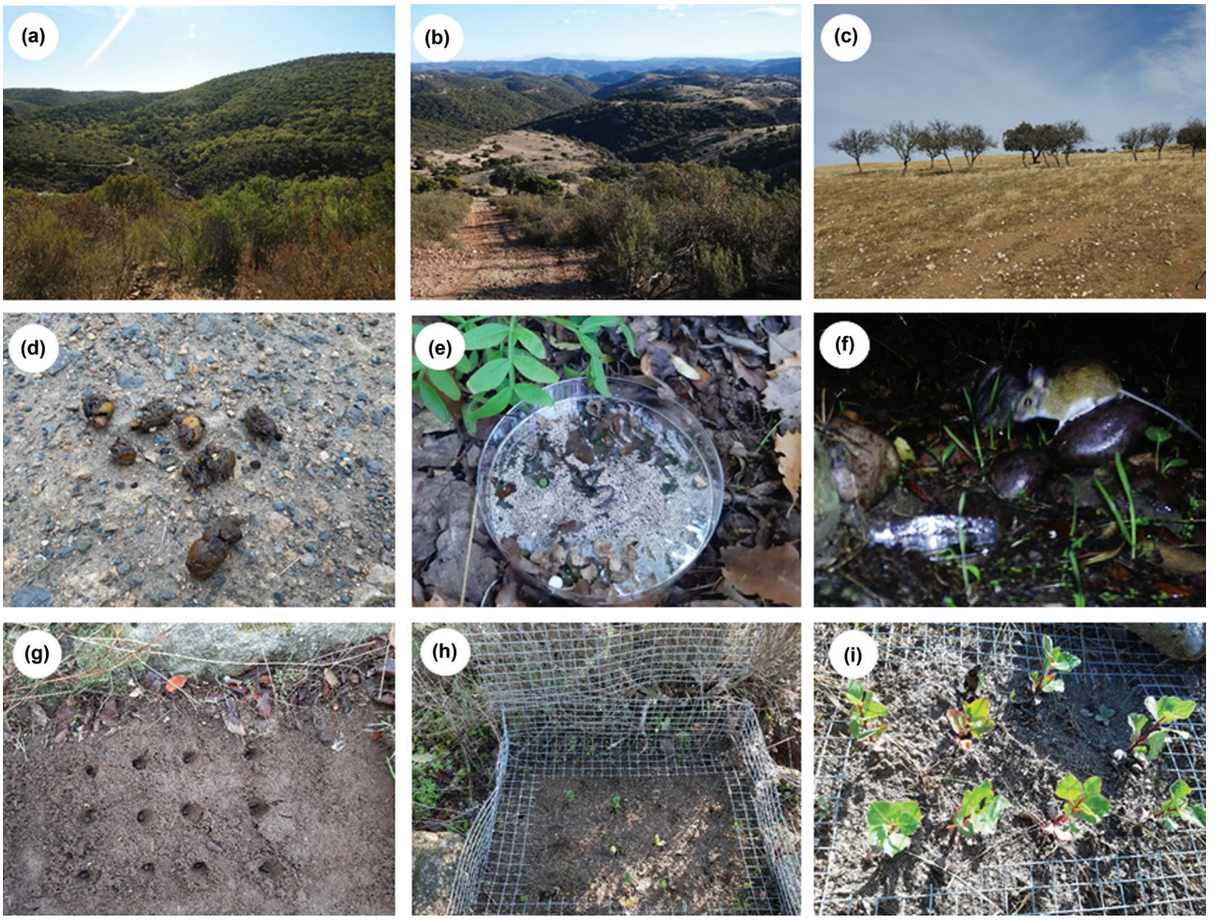



Figure 1. Photographs illustrating (a) the panoramic landscape perspective of a forest transect, (b) the landscape transition between forest and open habitats and (c) transect across open landscapes characterised by the lack of arboreal vegetation, with the exception of isolated individuals or clusters of Iberian pear *Pyrus bourgaeana*; (d) example of Iberian pear seeds dispersed by a red fox *V. vulpes* in our study area; (e) seed shells of Iberian pear predated by rodents in our seed predation experiment; (f) camera-trap image of a wood mouse *A. sylvaticus* eating deployed pear seeds. (g) Iberian pear seeds sowed in our experiment; (h) Iberian pear seedlings in the microsite 'shrub', under a rosemary *R. officinalis*; (i) first year seedlings of Iberian pear that survived at the end of the experiment.

deposition by mesopredators. We estimated post-dispersal predation rates of Iberian pear seeds in November 2020, coinciding with the species' seed-dispersal peak (Fedriani and Delibes 2009b). Seed removal rates were assessed through a field experiment in two localities: one with Iberian lynx presence and one control site without lynx. We placed 1152 Iberian pear seeds (extracted from ripe fruits collected in the field) in 144 Petri dish depots (eight seeds per depot; see the Supporting information for further details). As seed removal intensity varies across habitats and microsites (Hulme 1994), depots were distributed across six combinations of habitat type (forest and open) and microsite (rock, shrub and open), simulating dispersed seeds by mesopredators (Garrote et al. 2019, Fig. 1). In each habitat–microsite combination, we set up depots in six spatially independent plots (15 × 15 m) spaced 200 m apart – sufficient distance given rodents' limited home ranges (~1 ha; Rosalino et al. 2011). We placed eight seeds in each Petri dish at the start of the experiment, monitored them over five consecutive days, and recorded the total number of seeds removed (Supporting information). To account for potential seed removal by other consumers (e.g. ants, birds; Warzecha and Thomas Parker 2014, Suárez-Esteban et al. 2018), we installed 36 camera traps (Scoutguard SG562-C; white LED) at a subset of 25% of the seed depots. The camera traps confirmed that rodents *A. sylvaticus* were the sole seed predators in our experiment (Supporting information). Seed removal rates per depot were calculated as the total number of seeds removed after five days divided by the number of seeds initially placed.

### Seedling emergence and survival

To assess how habitat type and microsite influenced Iberian pear recruitment probability, we carried out a sowing experiment tracking seedling performance over one year. Assuming

that lynx presence does not directly affect Iberian pear seedling emergence and survival, we estimated these rates in a single locality within our study area. This experiment was replicated across ten spatially independent plots (200 m apart) of 15 × 15 m (details in the Supporting information). The experiment began in November 2020 and was monitored until February 2022, with visits to record seedling emergence and survival approximately every two months (details in the Supporting information). We sowed 360 Iberian pear seeds (12 per depot) across the same seed-dispersal habitats (forest and open) and microsites (rock, shrub and open) as mentioned earlier (Fig. 1). We calculated emergence rates as the number of seedlings emerged divided by the total number of seeds sown, and survival rates as the number of seedlings surviving at the end of the experiment divided by the total number of seedlings emerged.

### Transition probabilities estimates

To generate the input data for the structural equation models (below), we estimated stage-specific transition probabilities (TPs) under contrasting ecological scenarios based on our empirical data. TPs were calculated for seed survival, seedling emergence, and seedling survival as the ratio of individuals completing a stage to those entering the stage (Rey and Alcántara 2000, Balcomb and Chapman 2003, Garrote et al. 2022). Given the limited sample sizes used to estimate some mean observed TPs, we fitted Bernoulli distributions (n = 100) to the observed TPs for each lynx scenario, habitat and microsite. We then resampled randomly without replacement from each distribution, truncated by the standard deviation of the observed TP (Manly 2006), to introduce moderate stochasticity into the path analysis. To estimate how many individuals were retained at each stage under each habitat type, microsite and lynx scenario, we multiplied the stage-specific TPs by the corresponding number of individuals entering that stage. Specifically, post-dispersal seed survival rates were multiplied by the number of dispersed seeds to estimate the number of surviving seeds. Following the same approach, emergence rates were applied to the number of surviving seeds, and seedling survival rates to the number of emerged seedlings, thus estimating the number of recruits (i.e. surviving seedlings). Finally, we created a complete recruitment-stage dataset with the number of dispersed seeds, seeds that survived post-dispersal predation, emerged seedlings, and seedlings that survived their first year of life, for each habitat type, microsite and lynx scenario.

### Statistical analyses

We first fitted separate mixed models (GLMMs) using the 'lme4' package (Bates et al. 2020) for each life-cycle stage of the Iberian pear to describe the general patterns observed in each experiment independently. Responses were 1) the number of dispersed seeds, 2) seed predation, 3) seedling emergence and 4) seedling survival rates. Both seed dispersal (Poisson, link = log) and seed predation (binomial, link = logit) models included lynx presence, habitat, microsite, and their pairwise interactions. 'Locality' was included as random effect for seed dispersal and 'Plot' for seed predation. The models for seedling emergence and survival probability (binomial, link = logit) included only the habitat × microsite interaction and 'Plot' as random effect.

To integrate all ecological filters and assess the direct and indirect effects of lynx presence, habitat, and microsite on the Iberian pear recruitment, we applied structural equation modelling (SEM) to our recruitment-stage dataset. This analysis covered seed deposition by mesopredators through to seedling establishment (details in the Supporting information), based on confirmatory path analysis (Shipley 2000). We employed the 'piecewiseSEM' R package (Lefcheck 2016) to fit structural equations with GLMMs, specifying lynx presence/absence, habitat type (forest and open), and microsite (rock, shrub and open) as exogenous variables. Endogenous variables included: number of 1) mesopredator scats, 2) dispersed seeds, 3) post-dispersal surviving seeds, 4) emerged seedlings, and 5) first-year surviving seedlings. Poisson errors and the random effect 'Locality' was specified in all GLMMs. Standardised path coefficients were used to compare direct effects across different scales. We calculated standardised path coefficients separately for lynx presence and absence scenario in order to explore interactions between habitat, microsite type and lynx presence. Indirect and total effects were also computed to assess the relative importance of each exogenous variable on seedling survival (Shipley 2000, Supporting information). Marginal and conditional pseudo-$R^2$ were calculated to estimate the variance explained by each model. Residuals were inspected using the 'DHARMa' package ver. 0.4.6 (Hartig and Lohse 2022).

## Results

### Overall patterns

As previously reported in Burgos et al. (2024), a total of 1400 red fox and 175 stone marten scats were collected across the study area. The majority of scats – 64% for foxes and 91% for martens – were deposited outside lynx territories (back-transformed EMMean, [95% CI]) (no lynx: 8.42 (6.4–11.0) versus lynx: 4.16 [3.2–5.5]; $\chi^2 = 12.6$; $p < 0.001$). Among the scats, we found that 11% of those from foxes and 9% from martens contained Iberian pear seeds. In total, foxes and martens dispersed 1279 Iberian pear seeds, with 84% of these found in areas without lynxes (Fig. 2). The red fox dispersed significantly fewer seeds in open habitats in lynx-occupied territories (1.09, [0.2–5.8]) compared to open habitats in areas without lynxes (4.44, [0.9–22.7]; $\chi^2 = 7.63$, $p < 0.01$). The stone marten dispersed significantly fewer seeds within lynx territories and positively selected forests against open habitats (Table 1). The most common seed-arrival microsite for both mesopredators was the open microsite(Table 1), yet red foxes disproportionately dispersed more seeds in this microsite, particularly in lynx absence (no lynx: 10.2, [2.0–52.1] versus lynx: 2.67, [0.5–14.2]; $\chi^2 = 16.43$, $p < 0.001$).

Rodents removed 30% of the offered Iberian pear seeds during the post-dispersal seed predation experiment. The

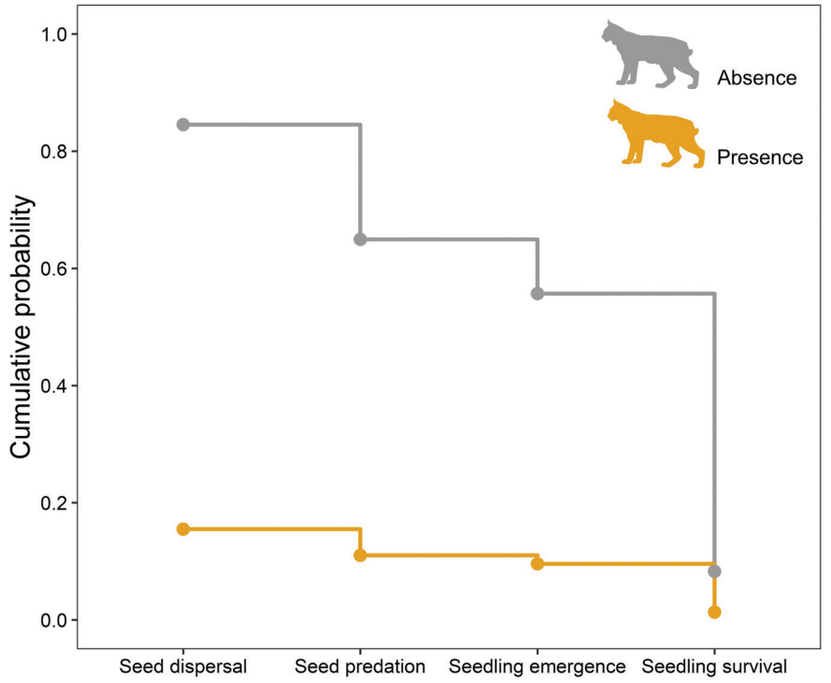



Figure 2. Stepwise cumulative probabilities of Iberian pear *Pyrus bourgaeana* seeds retained at each recruitment stage (seed dispersal, post-dispersal seed predation, seedling emergence and seedling survival) under scenarios with and without lynx presence. Points represent the proportion of individuals estimated after each successive ecological filter, calculated by multiplying the number of dispersed seeds by the estimated transition probabilities (TPs) for each life-cycle stage. Horizontal segments indicate the survival probability across stages, while vertical segments indicate the loss associated with each transition. Lines are shown separately for lynx presence (orange) and absence (grey) to highlight differences in cumulative survival trajectories. Seed dispersal data were obtained from Burgos et al. (2024), whereas post-dispersal stages (seed predation, germination and survival) were newly assessed in the present study.

seed predation rates for lynx presence and absence scenario were similar (Table 1). Rodents predominantly removed seeds in the shrub microsite (Table 1), regardless of habitat type and lynx presence. Of the seeds sown, 85% resulted in emerged seedlings. Emergence rates were rather consistent across habitats and microsites (Table 1). However, only 21% of emerged seedlings survived their first year (Fig. 2). Seedling survival was shaped by an interaction between habitat and microsite, with the highest survival observed within open habitats in the shrub microsite (open: 0.4

Table 1. Summary of overall patterns across the different field experiments and observations conducted in this study for the successive early life-cycle stages of the Iberian pear *Pyrus bourgaeana*. The table shows $\chi^2$-values for model predictors, back-transformed estimated marginal means with 95% confidence intervals for each factor level (in brackets), and marginal and conditional pseudo-$R^2$ ($R^2_m$ and $R^2_c$) from generalized linear mixed models (GLMMs). Bold $\chi^2$-values indicate significant effects ($p < 0.05$). Significant interactions are reported in the main text.

| | Response (EMMean, CI 95%) | | | | |
|---|---|---|---|---|---|
| Predictor | (a) Fox's seed dispersal | (a) Marten's seed dispersal | (b) Seed predation | (c) Seedling emergence | (d) Seedling survival |
| Lynx | $\chi^2 = 0.87$ | **$\chi^2 = 3.22$** | $\chi^2 = 0.17$ | | |
| Presence | 1.3 (0.2–7.1) | 0.01 (0.0–0.2) | 0.2 (0.1–0.6) | | |
| Absence | 4.4 (0.8–22.3) | 0.2 (0.01–1.8) | 0.1 (0.0–0.4) | | |
| Habitat | **$\chi^2 = 20.53$** | **$\chi^2 = 20.68$** | $\chi^2 = 0.24$ | $\chi^2 = 0.63$ | $\chi^2 = 2.36$ |
| Open | 2.2 (0.7–7.1) | 0.01 (0.0–0.1) | 0.2 (0.0–0.4) | 0.9 (0.8–0.9) | 0.2 (0.1–0.3) |
| Forest | 2.7 (0.8–8.6) | 0.1 (0.0–0.9) | 0.2 (0.1–0.5) | 0.9 (0.8–0.9) | 0.1 (0.1–0.2) |
| Microsite | **$\chi^2 = 263.25$** | **$\chi^2 = 8.43$** | **$\chi^2 = 20.24$** | $\chi^2 = 2.88$ | $\chi^2 = 3.09$ |
| Open | 5.2 (1.6–16.8) | 0.03 (0.0–0.4) | 0.1 (0.0–0.2) | 0.9 (0.8–0.9) | 0.1 (0.1–0.2) |
| Rock | 1.2 (0.4–3.8) | 0.02 (0.0–0.3) | 0.2 (0.1–0.4) | 0.9 (0.8–0.9) | 0.1 (0.1–0.3) |
| Shrub | 2.3 (0.7–7.4) | – | 0.4 (0.2–0.7) | 0.9 (0.8–0.9) | 0.3 (0.2–0.4) |
| $R^2_m$ | 0.19 | 0.44 | 0.13 | 0.11 | 0.31 |
| $R^2_c$ | 0.98 | 0.97 | 0.93 | 0.30 | 0.56 |

[0.2–0.6] versus forest: 0.2 [0.1–0.4]; $\chi^2 = 6.0$; $p < 0.05$). In lynx presence scenario, the estimated proportion of emerged seedlings surviving the first summer was around 1%, contrasting with the 8% of survival in absence of the apex predator (Fig. 2).

## Global path analysis

In our SEM model, a reduced number of fox and stone marten scats in the presence of lynx led to significantly fewer Iberian pear seeds being dispersed (Fig. 3A). This decrease in seed dispersal also resulted in fewer surviving seeds, emerged seedlings, and ultimately, surviving seedlings in the presence of lynx (Fig. 3A, Supporting information). Only two seeds were dispersed by the stone marten in the lynx presence scenario, indicating a collapse of its seed-dispersal service for the Iberian pear. In sites without lynx, the stone marten primarily deposited faeces and thus dispersed seeds (n = 58) in forest habitats (Supporting information).

The degree of cover at the seed-arrival microsite (lowest for 'open', intermediate for 'rock', and highest for 'shrub') negatively affected

the number of scats of both mesopredator species and the number of surviving seeds and emerged seedlings (Fig. 3A). No significant direct effect of lynx presence was found on post-dispersal seed predation by rodents (Fig. 3A). Lynx indirectly and negatively affected seedling survival, while habitat and microsite had both direct and indirect effects (Fig. 4A). Indirect effects of lynx presence accounted for up to 36% of the overall variation in seedling survival, while the overall habitat and microsite type effects explained 43 and 21% of the variation, respectively.

## Path analysis by predation risk scenario

We observed a subtle effect of habitat on faecal deposition in the absence of lynx (std. coeff. = 0.12; p = 0.02) when considering both carnivores together (Fig. 3C). This contrasts with

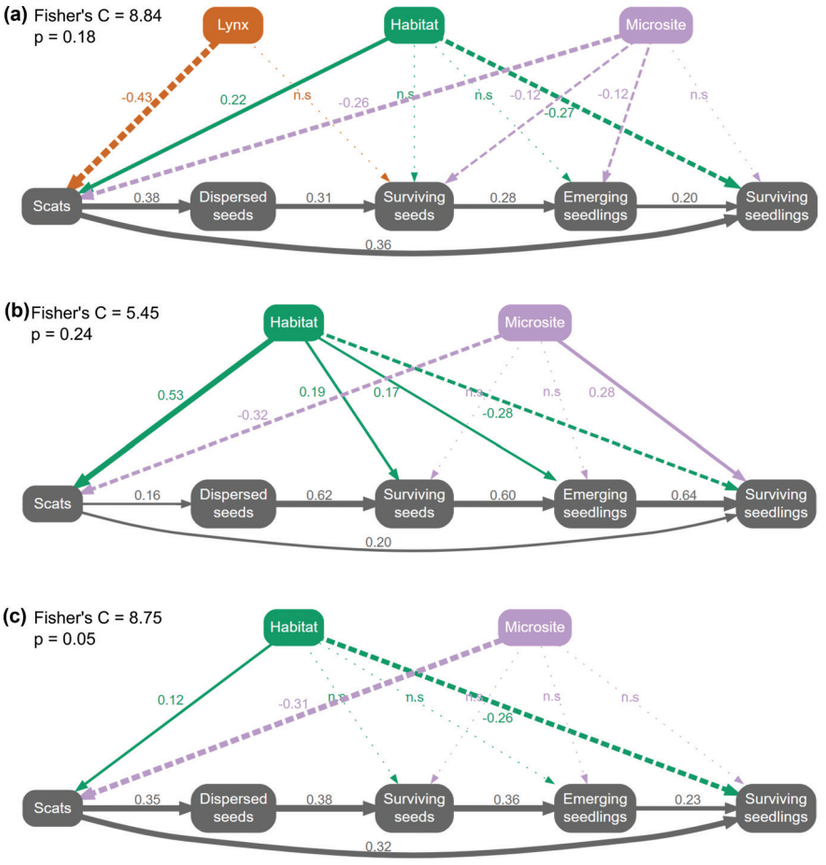



Figure 3. (a) Global, (b) only lynx presence and (c) only lynx absence path analysis of causal relationships between exogenous variables (lynx presence, habitat and microsite) and the vital phases of the life-cycle of an Iberian pear *P. bourgaeana* considering seeds dispersed by the red fox *V. vulpes* and the stone marten *M. foina* jointly. Exogenous variables were included as ordinal: lynx (0 = absence, 1 = presence), habitat (0 = open, 1 = forest), microsite (0 = open, 1 = rock, 2 = shrub). Arrow widths are proportional to the value of standardised path coefficients. Solid arrows show significant and positive direct effects, dashed arrows significant and negative effects and dotted arrows non-significant effects ($p > 0.05$). The number of scats and the seed dispersal values were taken from Burgos et al. (2024); the other life stages were measured specifically for this study.

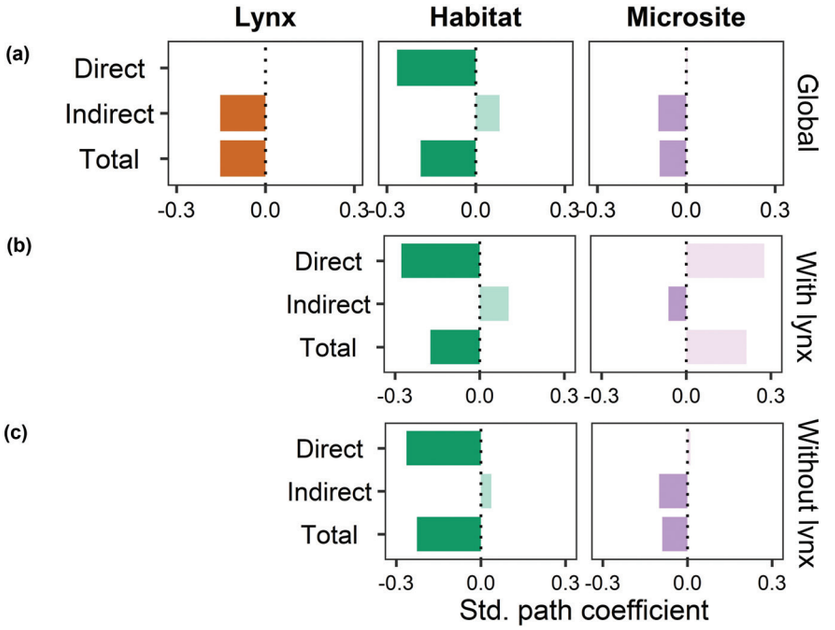



Figure 4. Direct, indirect and total effects of lynx, habitat and microsite on seedling survival from (a) the global SEM, (b) the lynx presence SEM, and (c) the lynx absence SEM considering Iberian pear seeds *P. bourgaeana* dispersed by the red fox *V. vulpe*s and the stone marten *M. foina* jointly. Direct effects are the standardised path coefficients directly linking seedling survival to the predictor variables. Indirect effects are the product of direct paths linking seedling survival to predictors through at least one intermediate variable. Total effects are the sum of direct and indirect effects for each predictor. Habitat and microsite were coded as ordinal variables increasing in cover (from open to forest and from open to shrub, respectively); thus, positive coefficients indicate positive effects of greater cover (i.e. forest habitats or shrub microsites), whereas negative coefficients indicate negative effects of greater cover.

the non-significant effect found in the model for fox alone (Supporting information). Open habitats directly promoted seedling survival in both predation risk scenarios (Fig. 3, 5). However, the opposite effect was found when evaluating indirect effects on seedling survival especially in presence of lynx (Fig. 4B, C), mainly due to increased fox-seed dispersal in forest habitats under lynx presence (Supporting information). The habitat of seed arrival accounted for 45% and 72% of the overall variation in seedling survival in lynx presence and absence scenario, respectively.

We also found a differential direct effect of microsite type on seedling survival between predation risk scenarios (Fig. 3B, C, 4B, C). In the presence of lynx, the degree of coverage at the microsite level significantly favoured seedling survival (Fig. 5), despite faecal deposition occurring mostly in open microsites (Fig. 5). In the absence of lynx, no significant differences in seedling survival were observed between microsites (Fig. 3B, C, 5). The microsite of seed dispersal explained 55% and 28% of the overall variation in seedling survival in lynx presence and absence scenario, respectively.

## Discussion

Our study pioneers the exploration of cascading effects triggered by apex predators on a fleshy-fruited tree reproductive performance, from seed dispersal by mammal carnivores to seedling emergence and establishment. By integrating both the quantitative and qualitative components of seed-dispersal effectiveness – i.e. the number of dispersed seeds and the probability that those seeds lead to successful recruitment (Schupp et al. 2010) – we provide a comprehensive assessment of how apex predator presence influences tree regeneration. Contrary to our predictions, open habitats actually enhanced Iberian pear seedling survival. Subordinate carnivores, influenced by the presence of a top predator, dispersed fewer Iberian pear seeds and biased the seed-arrival towards forests and open microsites, leading to reduced seedling recruitment. Similar predator-induced shifts in seed dispersal patterns were also reported for other fleshy-fruited plants in the same system (Burgos et al. 2024). Thus, seedling survival in lynx-occupied areas was compromised not only by the already documented lower dispersal rates, but also by seed delivery in less favourable sites for recruitment of this tree species. Despite the higher seed predation rates by rodents beneath shrubs, this microsite provided optimal conditions for seedling survival, particularly in open habitats. These results underscore the importance of examining spatial variations in the cascading impacts of apex predator recovery on plant population dynamics, especially in defaunated ecosystems where many large frugivores have been lost and predator-prey interactions are being restored through rewilding (Estes and Duggins 1995, Wilmers et al. 2012).

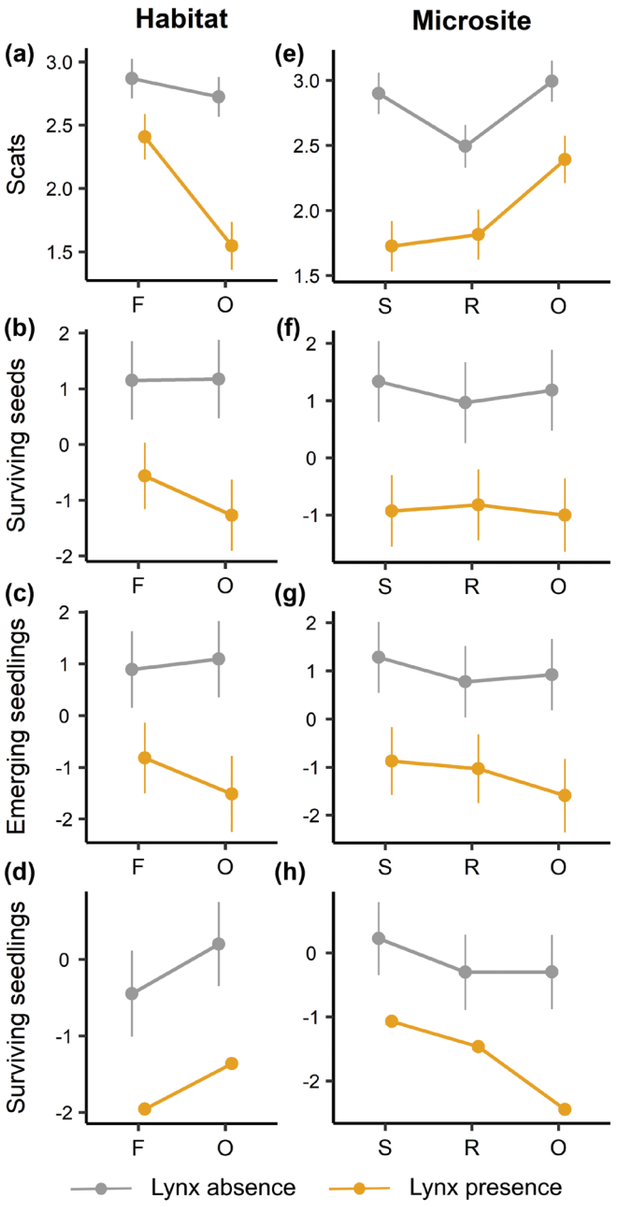



Figure 5. Linear predictions of the number of (a, e) mesopredator scats (*V. vulpes* and *M. foina* jointly), (b, f) surviving seeds, (c, g) emerging seedlings and (d, h) surviving seedlings of Iberian pear (*P. bourgaeana*) by habitat (F: forest, O: open) and microsite type (S: shrub, R: rock, O: open) in each predation risk scenario (grey: lynx absence; orange: lynx presence). Points represent marginal means from Tukey post hoc comparisons based on separate SEMs fitted for each predation risk scenario. Bars denote the respective delta standard errors (Supporting information). Habitat and microsite were ordered according to decreasing cover, from forest to open habitats and from shrub to open microsites Scat deposition data come from Burgos et al. (2024), while seed survival, seedling emergence and survival were newly recorded and analysed in this study.

### Mesopredator suppression effects on tree seed dispersal success

The Iberian pear relies on medium-sized carnivores for seed dispersal in Mediterranean ecosystems, where megafauna frugivores are absent (Fedriani and Delibes 2009b). These medium-sized predators are often suppressed by larger predators like the Iberian lynx (Jiménez et al. 2019, Burgos et al. 2023). Whereas mesopredators dispersed many seeds outside lynx territories, their dispersal service collapsed in lynx-inhabited areas, especially for martens (Burgos et al. 2024). In this study, we found that seed dispersal of the Iberian pear by stone martens declined in lynx-occupied areas, in line with Burgos et al. (2024) reported for the entire fleshy-fruited plant community. This aligns with findings that stone martens are highly sensitive to predation risk (Virgós et al. 2020, Burgos et al. 2023) and thus, top predators can have a stronger negative impact on the quantity and quality of seed dispersal by martens.

Behaviourally-mediated trophic cascades often led subordinate carnivores to alter their behaviour to avoid costly encounters with apex predators (Schmitz et al. 1997, Fedriani et al. 2000). In our study area, Iberian pear trees often occur in open habitats, which are risky for mesopredators. This is consistent with Burgos et al. (2022), who found reduced fox visitation to Iberian pear fruiting trees in the presence of lynxes. Our path analysis confirmed that foxes dispersed fewer seeds in open habitats only under predation risk, ultimately reducing seed-dispersal effectiveness in this scenario (Schupp et al. 2010, Selwyn et al. 2020). Mesopredators showed a preference by open microsites for faecal deposition in overall, reflecting typical territorial behaviour (Martínez et al. 2008, Fedriani and Delibes 2009b, Suárez-Esteban et al. 2013). Indeed, García-Cervigón et al. (2018) noted that carnivores disproportionately deposit more seeds in open microsites. In our study, this seed-dispersal behaviour was particularly accentuated for foxes in areas without lynxes, possibly because they experienced reduced fear of detection and moved more freely through open interspaces (Fedriani et al. 2000, Pasanen-Mortensen et al. 2013). Such changes in the spatial pattern of seed deposition are critical, as the seed arrival microsite is a major determinant of post-dispersal seed survival and plant recruitment (García et al. 2005, Escribano-Ávila et al. 2013, González-Varo et al. 2015, Donoso et al. 2017).

### Post-dispersal seed survival in a landscape of fear

Post-dispersal seed predation is often positively correlated with the abundance and activity of seed predators (Díaz 1992, Fedriani and Manzaneda 2005, Wang 2020, Bartel and Orrock 2021). In our study, we did not detect a significant effect of lynx presence on seed predation rates by rodents. Nonetheless, previous long-term research in the same area (Burgos et al. 2023) found a higher abundance of seed-eating rodents in lynx territories, where mesopredator populations were up to ten times lower compared to areas without lynx. In particular, the species showing the strongest increase in lynx areas was the garden dormouse *Eliomys quercinus*, a species that hibernates and is much less active during

autumn and winter. Therefore, its peak activity likely occurs outside the main seed-dispersal period of the Iberian pear (autumn–winter). Nonetheless, the lack of a detectable effect may also reflect the short temporal scope of our experiment, conducted in a single season. A longer or seasonally replicated design might have revealed stronger cascading effects on seed predator dynamics, as observed in other systems (Wright et al. 2000, Pender et al. 2013, Galetti et al. 2015).

Seed predation often varies among habitats, which may reflect seed predator preferences (Christianini and Galetti 2007, García et al. 2011). Interestingly, our path analysis indicated that habitat effects on post-dispersal seed survival were important only in lynx presence scenario. Forest habitats impacted positively post-dispersal seed survival in presence of the apex predator, likely due to intense faecal deposition in this habitat type and therefore, the higher seed dispersal by foxes when coexisting with lynx (Burgos et al. 2024). Microsite of seed arrival also strongly influences seed predation (Hulme 1994, Matías et al. 2009). Rodents preferentially predated Iberian pear seeds under bushes, in line with other studies in Mediterranean forests, probably due to a lower perceived predation risk (Rey et al. 2002). Open microsites were the most favoured by mesopredators for seed deposition, but in these sites seed predation rates were generally lower than under shrubs, consistent with other Mediterranean plants (e.g. *Corema album* and *Juniperus phoenicea;* Suárez-Esteban et al. 2018).

### From frugivory to recruitment: cascading effects on seedling establishment

The loss of key mutualistic interactions, such as seed dispersal by mesopredators, can trigger trophic cascades affecting plant reproductive cycles (Traveset et al. 2012, Rogers et al. 2021). The decline in stone marten dispersal services due to the lynx presence may jeopardize the persistence of the Iberian pear, a scarce tree reliant on such mutualistic interactions. Fedriani et al. (2020a, 2023) demonstrated that defaunation scenarios affecting key seed dispersers, such as foxes and badgers, altered demographics of this fleshy-fruited tree, by limiting seed arrival to vacant habitats (e.g. old fields). Thus, although we found that foxes continued dispersing seeds under high predation risk, subtle functional differences among frugivores (e.g. habitat-use patterns or dispersal distances; Jordano et al. 2007, Escribano-Ávila et al. 2014) can be crucial for the fate of post seed-dispersal tree stages.

In the presence of the apex predator, Iberian pear seeds primarily reached forest habitats driven by foxes shifting their dispersal. According to our path analysis, forests directly reduced seedling survival, contrary to our expectation that forest cover would provide better conditions such as a higher shade and humidity for seedlings (Gómez-Aparicio et al. 2004, Pulido and Díaz 2005). However, we also found an indirect positive effect of forest habitats on seedling survival, due to more seeds being delivered to forests under lynx presence, partly compensating their lower suitability. These habitat shifts contributed to the indirect effect of lynx presence in the path analysis, which explained up to 36% of the variation in seedling survival, underscoring the large contribution of behaviourally driven pathways to recruitment outcomes. This finding highlights the importance of trophic cascades on early plant-life stages, particularly on first summer seedling survival, typically regarded as the most critical stage in plant recruitment (Fedriani and Delibes 2009b). In addition, our results demonstrate that the Iberian pear often grows in open habitats not only because it is a frequent habitat of seed delivery by mammals (Fedriani and Delibes 2009a, Fedriani et al. 2010), but also because this habitat seems to provide more suitable conditions for its recruitment (e.g. high light availability, low competition), at least in early stages. This interpretation is consistent with previous studies showing that some *Pyrus* species are strongly light-dependent, such as *P. pyraster* in forest edges (Gonzalez et al. 2010), and highlighting the occurrence of *P. bourgaeana* in open, treeless habitats and its heliophilous character (Arenas-Castro 2011). Thus, the impact of post-dispersal processes are expected to spatially vary within population in the landscape of fear (Calviño-Cancela 2007), being highest where recruitment is seed limited due to the presence of an apex predator.

Beyond habitat-level differences, seedling establishment was also strongly influenced by fine-scale processes at the microsite level. While open habitats favoured seedling survival, they also had high seed predation rates in microsites optimal for plant establishment (e.g. shrubs). This creates a seed–seedling conflict (Schupp 1995, Garrote et al. 2022): the microsites where rodents remove more seeds are also those most suitable for seedling survival, reducing the chances that seeds ever reach the next stage. This dynamic may hinder Iberian pear expansion (Fedriani et al. 2018, 2020a), especially under scenarios of apex predator recovery. In the presence of lynx, Iberian pear recruitment seemed particularly sensitive to fine-scale processes as seed arrival beneath shrubs (acting as nurse plants) enhanced seedling survival, especially in open habitats (Gómez-Aparicio et al. 2004, Mendoza et al. 2009, Perea et al. 2020). Therefore, in this scenario, where seed delivery is limited by dispersers, the availability of suitable microsites becomes especially critical. Variation in the number of dispersed seeds and the suitability of the seed-arrival sites can strongly affect plant recruitment across different spatial and temporal scales (Schupp et al. 2010, Garrote et al. 2022). For the Iberian pear, apex predators appear to restrict recruitment, but assessing whether similar cascading effects occur at the community level remains challenging. Plant species often differ in their habitat requirements and seed dispersers, which vary in both their habitat use and seed dispersal patterns (Maron and Pearson 2011, Donoso et al. 2017, Fedriani et al. 2020a).

Other mammal seed-dispersers not limited by lynxes (e.g. badgers) or large avian frugivores like the Iberian magpie *Cyanopica cooki* could partially compensate for reduced dispersal services (Fedriani et al. 2024) due to lynx presence. Many Mediterranean plants also rely on birds for seed dispersal (e.g. *A. unedo* or *Juniperus* sp.; Herrera 1998, Santos et al. 1999, García 2001). However, different frugivores play distinct roles in seed dispersal, making intra-guild

compensation variable and challenging to predict (González-Varo et al. 2015, 2023, Fedriani et al. 2020a, 2023). In this line, Escribano-Ávila et al. (2014) found that foxes and martens played a key role in colonization processes for *Juniperus thurifera*, due to the major seed dispersal away from the maternal surrounding, in contrast with the local seed dispersal of thrushes. Thus, since frugivores differ in subtle but key aspects of the seed dispersal process (Escribano-Ávila et al. 2013, Rumeu et al. 2020, Fedriani et al. 2023), the potential for intra-guild compensation to ameliorate the loss of certain species can be very variable in space and time.

## Concluding remarks

Our findings underscore the importance of considering cascading effects throughout the plant life cycle, particularly in human-altered ecosystems. Habitat and microhabitat-specific seed dispersal dynamics (Fedriani et al. 2023) must be integrated into assessments of frugivore ecosystem services to understand the impacts of ecological disturbances in heterogeneous landscapes. Subtle behavioural differences among seed dispersers can cause significant functional variations in seed-dispersal effectiveness, which are crucial for predicting the effects of frugivore loss on plant demographics. In our system, direct effects of lynx presence on mesopredators' behaviour – and thus on seed dispersal patterns – combine with indirect effects on seed dispersal quality, ultimately influencing the recruitment success of the Iberian pear. Although our study combines field experiments with an observational comparison of localities with and without lynx within a naturally recolonized population, our results offer valuable insights for rewilding initiatives. In such contexts, especially where large frugivores are absent or declining, apex predator reintroductions may indirectly affect plant regeneration, emphasizing the need to anticipate and monitor cascading ecological effects when restoring predator communities. We recommend that conservation managers and policymakers carefully evaluate how apex predator rewilding may reshape plant–animal interactions, particularly in systems where mutualistic dispersal networks are already eroded. Monitoring not just predator–prey antagonistic interactions but also mutualistic processes will be essential to guide adaptive management strategies and avoid unintended consequences for plant regeneration.

*Acknowledgements* – We thank the Sierra de Andújar Natural Park and Organismo Autónomo de Parques Nacionales (OAPN) for the corresponding authorizations and the Foundation Amigos del Lince Ibérico y del Águila Imperial for supporting this study in private lands. We also thank to J. Hernández-Hernández, J. Rodríguez-Siles and I. Cancio for their field sampling assistance.
*Funding* – This study was funded by the Spanish Ministry of Science, Innovation and Universities with the grant CGL2017-84633-P and the fellowship FPU17/04375.
*Conflict of interest* – The authors declare no conflict of interest.

### Author contributions

**Tamara Burgos**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (supporting); Supervision (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jose María Fedriani**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Supervision (equal); Visualization (supporting); Writing – review and editing (equal). **Gema Escribano-Ávila**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Supervision (equal); Visualization (supporting); Writing – review and editing (equal). **Emilio Virgós**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (equal); Visualization (supporting); Writing - review and editing (equal).

### Data availability statement

Data are available from the Dryad Digital Repository: https://datadryad.org/dataset/doi:10.5061/dryad.2547d7x2r (Burgos et al. 2025).

### Supporting information

The Supporting information associated with this article is available with the online version.

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