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Research

Intertwined effects of defaunation, increased tree mortality and density compensation on seed dispersal

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Ecography

43: 1352–1363, 2020

doi: 10.1111/ecog.05047

Subject Editor: Douglas A. Kelt

Editor-in-Chief: Miguel Araújo

Accepted 4 May 2020



Contemporary defaunation has profound ecological consequences ranging from local or even global co-extinctions of interacting species to the loss of ecosystem functions and services critical for humanity. Other components of global change (climate change, introduced pests, land use changes) are also harming ecosystem functioning by augmenting tree mortality worldwide. Defaunation and increased tree mortality often coincide in many human-altered ecosystems but whether they interact, leading to non-additive effects on ecosystem functioning, remains largely unknown. However, under some ecological circumstances, the decline or extirpation of one species due to defaunation can be neutralized by increases in the abundance of some functionally similar species (i.e. ‘density compensation’). We combined long-term field data with individual-based modelling to investigate the potential interactive effects of seed disperser loss, increased tree mortality and density compensation on seed dispersal in a heterogeneous landscape. Our simulation experiments showed that both stressors markedly limit not only the quantity of seed dispersal but also its quality since the impact on seed dispersal strongly varied among habitat types that differ strikingly in suitability for tree establishment. Density compensation had a marked positive effect on seed dispersal which, however, was largely limited under increased tree mortality. The combined negative effects of defaunation and increased tree mortality on seed dispersal were lower than the expected additive effect. This highlights the need to account for the joint operation of multiple stressors to accurately predict the impacts of global change on the link between biodiversity and ecosystem functioning.

Keywords: droughts, ecosystem services, global change, individual-based modeling, *Pyrus bourgaeana*, sink habitats

Introduction

Contemporary defaunation has profound ecological consequences ranging from local or even global co-extinctions of interacting species to the loss of ecosystem



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functions and services critical for humanity (Dirzo et al. 2014, Young et al. 2016, Emer et al. 2019). Carbon sequestration, pollination and seed dispersal stand out among the essential ecosystem services threatened by the current wave of defaunation (Potts et al. 2010, Galetti et al. 2013, Bello et al. 2015). Other components of global change (climate change, introduced pests, wild fires) are also harming ecosystem functioning by promoting tree mortality in many human-altered habitats (Linares et al. 2009, Van Mantgem et al. 2009, Carnicer et al. 2011, Boyd et al. 2013). Defaunation and increased tree mortality often co-occur in human-altered ecosystems (Lewis et al. 2015, Trumbore et al. 2015) and thus are likely to interact in amplifying or ameliorating the effect of each other on ecosystem functioning (Didham et al. 2007, Antikueira et al. 2018, Galic et al. 2018). Given the importance of biodiversity for the maintenance of ecosystem functions and the services that they underpin (Oliver et al. 2015, Schleunig et al. 2015), a comprehensive understanding of such potential interactive effects is crucial. Surprisingly, however, whether and how these two stressors interact and lead to potentially non-additive effects on ecosystem functioning remains largely unknown (but see Granados et al. 2018).

Seed dispersal is a critical demographic process that influences plant dynamics, the assemblage of entire communities, and the functioning of many ecosystems (Nathan and Muller-Landau 2000, Schupp et al. 2010, Bascompte and Jordano 2013). Large and medium-sized frugivorous vertebrates (usually mammals and birds) are key ecosystem elements responsible of seed dispersal of many large-fruited plant species (Herrera 2002, Fleming and Kress 2013). In human-altered habitats, these frugivorous vertebrates have frequently suffered a history of persecution and exploitation that perpetuates contemporarily, causing marked population declines and local extinctions (Peres and Dolman 2000, Ripple et al. 2014). As a consequence, plant populations relying on frugivorous vertebrates for seed dispersal experience reductions of their seed rain, impoverishments of the diversity of habitats of seed arrival (Wright et al. 2000, Carlo et al. 2013), declines in recruitment and establishment (Caughlin et al. 2015, Pires et al. 2018), and eventually modifications of their ranges and spatial distributions (Rotllan-Puig and Traveset 2016, Bagchi et al. 2018). Furthermore, these same plant populations inhabiting defaunated areas are often seriously impacted by human-induced mortality (Lewis et al. 2015, Trumbore et al. 2015). Although the isolated impact of these two stressors (*sensu* Darling and Côté 2008) on ecosystem functioning have been often investigated, we are not aware of any study on their joint impact on seed dispersal.

Under some ecological circumstances, the decline or extirpation of one seed dispersing species can be neutralized by increases in the abundance of some similar species (i.e. 'density compensation'; Peres and Dolman 2000, Larsen et al. 2005). In the case of disrupted fruit–frugivore interactions, there is evidence that both supports (Cordeiro and Howe

2003, Elmqvist et al. 2003) and rejects (Donatti et al. 2009, Bueno et al. 2013, Fricke et al. 2018) this compensation hypothesis. Clearly, the extent to which the reduction of a seed disperser population can be compensated by a second population largely depends on their level of functional redundancy (*sensu* Zamora 2000). For instance, vertebrate seed dispersers in heterogeneous landscapes frequently disperse seeds to habitats that differ in suitability for plant establishment and recruitment (Gómez et al. 2004). Thus, partial rather than complete density compensation may be expected following severe population decline of a given seed disperser species if the remaining disperser species in the community deliver seeds with different frequencies into different habitats than the lost disperser species. However, models of seed dispersal seldom account for the loss of seeds to unsuitable (e.g. sink) habitats, despite the often stringent conditions necessary for seed germination and seedling survival and establishment (Levin et al. 2003, Anderson et al. 2011, Ehrlén and Morris 2015).

The intertwined effects of defaunation, increased tree mortality and density compensation on seed dispersal kernels (*sensu* Bullock et al. 2017) and seed rain critically depend on the population characteristics and biology of the interacting plant and animal species. For example, the patterns of seed disperser movement and habitat and microhabitat use, as well as seed retention times in the gut, are essential aspects to accurately predict levels of functional redundancy between species (Pegman et al. 2017, Rodríguez-Pérez et al. 2017, Fedriani et al. 2018) and thus, the likelihood of density compensation. Predicting seed rain in such complex systems represents a major research challenge that demands integrative approaches that go beyond field studies. Fortunately, recent techniques of individual-based and spatially explicit modelling (Grimm et al. 2005, Railsback and Grimm 2019) allow for an integration of diverse sources of information into a simulation model. This provides means for investigating – through simulation experiments – how the pattern and intensity of seed rain are determined by the density and distribution of reproductive plants in combination with the abundance of dispersers, their behaviour and their physiology.

In this study, we investigate the intertwined effects of defaunation, increased tree mortality and density compensation on the overall seed rain and habitat-specific seed dispersal by combining comprehensive long-term field data with an individual-based, spatially explicit simulation model (called 'DisPear'; Fedriani et al. 2018). To our knowledge, this is the first study to investigate these factors simultaneously. We applied our model to the Iberian pear *Pyrus bourgaeana*, a mammal-dispersed tree, in a heterogeneous human-altered landscape in Mediterranean Spain (the Doñana World Biosphere Reserve). In this area, several potential tree seed dispersers have gone extinct (Fedriani et al. 2010) and extant dispersers, mostly the Eurasian badger *Meles meles* and the red fox *Vulpes vulpes*, experience intensive human-related

mortality due to poachers, road kills, etc. (Fedriani 1997, Revilla et al. 2001, Authors unpubl.). Because these two disperser species differ in their levels of frugivory and relative use of available habitat types (Fedriani et al. 1999), density compensation is not expected to fully ameliorate the detrimental effects of defaunation on seed dispersal.

We first describe patterns of seed dispersal by foxes and badgers under a baseline scenario representing the observed disperser densities and tree mortality levels. Then, we compared the baseline results with those from scenarios where fox or badger numbers are decreased, tree mortality is increased and under scenarios combining both stressors. We also simulated scenarios where population declines of a given disperser species are compensated with increases in numbers of the second disperser species. Specifically, we aimed to address the following three questions: 1) does fox and badger loss reduce the number of *P. bourgaeana* dispersed seeds and, if so, is the reduction comparable between disperser species in terms of seed dispersal into different habitat types? 2) Does density compensation counteract the impact of defaunation on seed dispersal and, if so, does such compensation occur in a similar extent across habitats? 3) Do the effects of defaunation

and increased tree mortality on seed dispersal interact and, if so, do they amplify or ameliorate each other?

Material and methods

Study system

Our study site is located within the Doñana World Biosphere Reserve, SW Spain (elevation 0–80 m a.s.l., Supplementary material Appendix 1). The climate is Mediterranean sub-humid, characterized by dry, hot, long summers (June–September) and mild, wet winters (November–February). Doñana’s heterogeneous landscape is comprised of eight habitat types differing in vegetation cover, density of *P. bourgaeana* and level of human interferences (Fedriani et al. 1999). Nonetheless, for the purpose of this study, they have been grouped into four main habitat types (Fig. 1A): 1) Mediterranean scrubland is comprised mainly of *Pistacia lentiscus* shrubs with variable cover by the shrubs of *Halimium halimifolium* and *Chamaerops humilis* and with scattered *Quercus suber* and *Pinus pinea* trees (this habitat holds

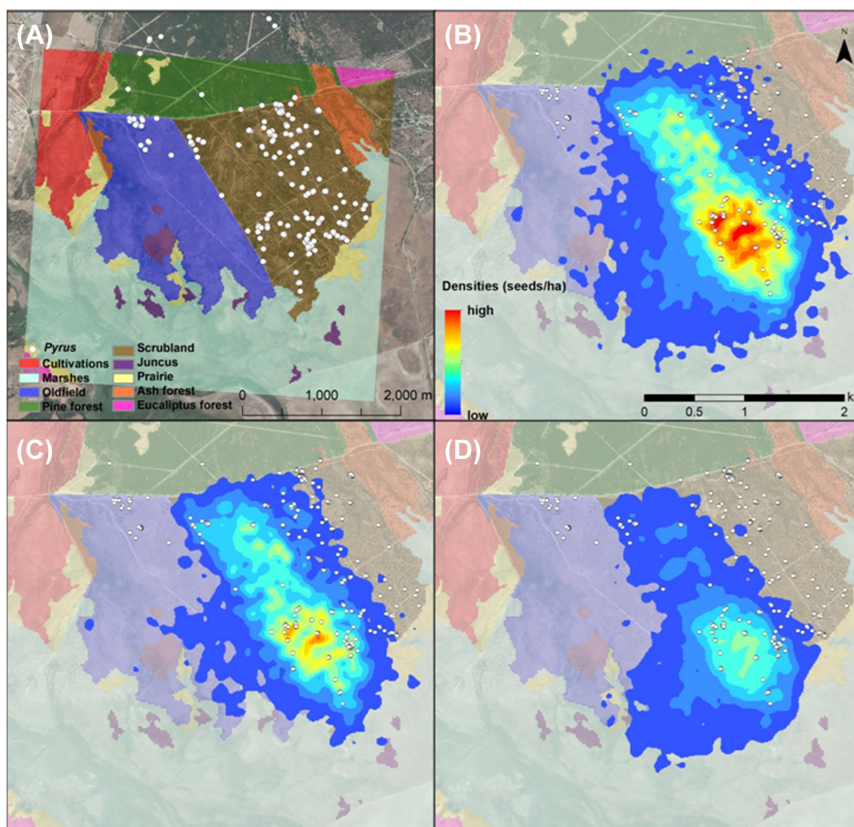


Figure 1. (A) Detailed view of the study site showing the different habitat types, (B) total seed rain for the baseline scenario (i.e. neither defaunation nor increased tree mortality), (C) partial seed rain considering only Eurasian badger dispersal events and (D) partial seed rain considering only red fox dispersal events. The white disks represent the location of observed reproductive trees. The colour gradient of the seed rain indicates the density of dispersed seeds, ranging from very low (pale blue) to very high density (red). Other colours represent different habitat types (gray, marshes; reddish, cultivations; beige, prairies; green, pine plantations; dark brown, Mediterranean scrubland; pale brown, ash forest; pink, Eucalyptus forest; pale purple, oldfield; dark purple, junco patches).

most adult *P. bourgaeana*), 2) an oldfield that currently is an open area of *Juncus* spp. with some *H. halimifolium* and *Staracanthus genistoides* bushes, and scattered *Q. suber* and *Olea europaea*, 3) the marshes are open areas flooded in winter and thus unsuitable for most terrestrial plants (e.g. *P. bourgaeana* has never been observed within this habitat) and 4) 'other habitats' comprising patches of pine, ash and *Eucalyptus* spp. forests, prairie and cultivations. A detailed description of the study area habitats and details on *P. bourgaeana* biology are provided in the Supplementary material Appendix 1.

Red foxes and badgers feed intensively on Iberian pear fruits during the autumn and early winter, and they disperse a variable number of seeds into each habitat type (Fedriani et al. 2018, Garrote et al. 2018). Habitat use and movements of both individual foxes (n=31) and badgers (n=17) has been studied in detail at our study site by telemetry (e.g. 24-h periods, with dispersers being located at 1-h intervals; Fedriani et al. 1999, Revilla et al. 2001). In general, during daytime both foxes and badgers are inactive and hidden in their dens at the Mediterranean scrubland, while during sunset they tend to move towards open habitats (e.g. oldfield, marshes) where they remain active during most of the nighttime. Nonetheless, they differ in the relative use of the different habitat types and thus in the habitat-specific seed rain they generate (Fedriani et al. 2018). Mortality of both foxes and badgers is frequent due to illegal poaching, road kills and other human-related causes (Fedriani 1997, Revilla et al. 2001, Authors unpubl.).

The 'DisPear' model

'DisPear' is a mechanistic, spatially explicit, individual-based model implemented in NetLogo 5.2.0. A complete, detailed model description, following the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, 2010, 2020, Railsback and Grimm 2019) is provided in the Supplementary material Appendix 2. It includes information about the rationale and data underlying all model assumptions.

The overall purpose of our model is to simulate *P. bourgaeana* seed rain in the study area. Specifically, the seed rain of *P. bourgaeana* emerges from the interaction between the physiological traits, habitat use and foraging behaviour of its mammalian seed dispersers, and the abundance and spatial distribution of fruiting trees. The model was developed, parameterized and tested following the pattern-oriented framework (sensu Grimm et al. 2005) as detailed by Fedriani et al. (2018). To obtain a model sufficiently realistic for this purpose, we integrated observed patterns in dispersers' movement and habitat use, and in the abundance, spatial distribution and clustering of fruits and feces into model design and inverse parameterization (Fedriani et al. 2018). All these patterns (46 in total) were based on extensive field and experimental data collected over two decades.

The model includes the following six entities: 1) square grid patches of 20×20 m² that belong to a given habitat type (oldfield, scrubland, marshes and 'other habitats'),

2) individual seed dispersers (foxes or badgers) that move across the landscape, 3) spatial-groups that represent the area where the social groups of dispersers centre their activities, 4) fruiting pear trees, 5) fruits that are produced by pear trees and become available to seed dispersers once they ripen and fall and 6) disperser feces that are delivered by dispersers and contain the seeds (see Supplementary material Appendix 2 for details).

Each time step in the model represents one hour within a 75-d period that corresponds to the 'dispersal season' (mid-September to the end of November) when ripe *P. bourgaeana* fruits are available to dispersers (Fedriani et al. 2012). The model is run for 25 yr, with each year represented by the 75-d dispersal season only. The model's spatial extent (total area is ~1840 ha) is a rectangular landscape of 221×208 patches (Fig. 1).

The most important processes of the model, which are repeated every time step during a fruiting season – except fruit drop, which occurs only at the beginning of the day (i.e. once every 24 time steps) – are: 1) fruiting trees drop 2–4 ripe fruits once per day that become available to dispersers; 2) fallen ripe fruits age and those older than three days become unavailable to dispersers, while fruits previously ingested by dispersers and not yet defecated increase their gut retention time; 3) dispersers move to preferred habitats according to circadian patterns based on extensive hourly telemetry data (Fedriani et al. 1999, Supplementary material Appendix 2–3). Dispersers move most of the night but tend to come back to their den during sunrise where they generally remain inactive during daytime. The movement submodel is based on hourly telemetry data, i.e. on observed distributions of step lengths and directions; 4) based on empirical probabilities describing foraging habits, individuals 'jump' in the model a given distance in a given direction, but we allow foraging within a 'corridor' along the path taken. We let them eat fruits with certain probabilities if there is a fruiting tree with available fallen fruits in the corridor and if the dispersers are not satiated; 5) dispersers might also defecate depending on the gut retention times of ingested fruits. Foxes defecate at a randomly chosen patch within their movement corridor whereas badgers preferentially defecate in a latrine if one exists within the movement corridor; if none exists, they initiate a new latrine (Fedriani and Wiegand 2014). At the end of a fruiting season, tree mortality takes place, live trees set their new initial crop, and existing fallen fruits and defecated feces are removed from the simulation. Further details on the model processes are provided by Fedriani et al. (2018) and the Supplementary material Appendix 2.

One particularly important design concept for the objectives of this study is the way in which we represented interaction among entities. Dispersers do not interact directly with each other (Fedriani et al. 1999). Trees and dispersers interact in a sense that dispersers eat fruits and thereby change their gut content. The number and spatial distribution of dispersed seeds emerge from the interaction of fruiting *P. bourgaeana* trees and dispersers and thus depend on the

number and location of trees and the number of individuals of each disperser species, which differ in their habitat use, seed retention times and movement behaviour, and hence in their probabilities of finding existing trees and delivering seeds in each habitat type. Dispersers interact indirectly with each other via exploitative competition for fruits, especially when the number of fruiting trees is low.

At the beginning of the simulation, the model is initialized in four steps: 1) habitat type of patches and location of the fruiting trees are defined through an input file; 2) the crop size of each fruiting tree is randomly drawn from a Poisson distribution parameterized based on observed field data; 3) the dispersers' spatial groups and associated home ranges are defined; 4) dispersers are created and located following rules described in the ODD. In simulations including density compensation, a number of seed dispersers (defined by the corresponding defaunation mortality scenario) are randomly removed, and are subsequently replaced at the same spatial point by individuals of the second disperser species to an extent set by the compensation level.

Simulation experiments

We investigated the outcome for *P. bourgaeana* seed dispersal under different scenarios of defaunation, tree mortality and density compensation by means of simulation experiments. To identify the combination of factor levels most markedly impacting *P. bourgaeana* seed rain, we used a full factorial design (2 disperser species \times 3 defaunation levels \times 2 tree mortality levels \times 3 compensation levels).

This analysis involved first a baseline scenario reproducing the densities of both seed dispersers (five badgers and five foxes) and reproductive trees (328 individuals) observed in the field (Fedriani et al. 2018). Second, we simulated three scenarios of defaunation by decreasing the density of one carnivore species by 40% (mild defaunation; 2 individuals removed), 80% (intermediate defaunation; 4 individuals removed) and 100% (complete defaunation). Third, we simulated alternative scenarios of tree mortality by setting two levels of annual mortality. Our long-term monitoring of *P. bourgaeana* in Doñana indicates that adult trees mostly died due to drought stress (during summer) and winter storms (when they fall) at an initial annual rate of \sim 0.5%, though this rate is increasing rapidly (Authors unpubl.). Thus, we specified a baseline annual mortality of 0.5% and an augmented one of 7% under conditions of intense perturbations (droughts, storms, pests). This latter scenario of increased tree mortality was run both alone and in combination with defaunation. Recruitment of adult trees in Doñana is very infrequent (e.g. no new reproductive tree has been recorded during the last 25 yr in our study area). Thus, we did not include recruitment of new reproductive trees during our 25-yr simulated periods. Finally, to investigate the consequences of different scenarios of density compensation, we replaced a fraction of the removed dispersers by individuals of the second disperser species in proportions of 0 (no compensation), 0.5 (partial compensation) and 1 (total compensation).

For each combination of factor levels (18 per disperser species), we ran 100 simulations, with each replicate comprising 45 000 time steps, or hours (i.e. 25 fruiting seasons \times 75 d \times 24 h). We analyzed the joint effect of defaunation, tree mortality and compensation on the overall seed rain as well as on five additional model outputs or response variables: total number of dispersal events (i.e. feces containing seeds) and number of dispersal events into each of the four habitat types after 25 yr.

Finally, following Darling and Côté (2008), the effect of defaunation and increased tree mortality (factors) on seed dispersal was measured as the ln-transformed response ratio:

$$RR = \ln \frac{\text{Treatment}}{\text{Baseline}}$$

where Treatment and Baseline are the mean number of dispersal events under different treatments (single or combined factors) and the baseline scenarios, respectively. We calculated for each isolated factor, and for their additive effects, the 95% confidence limits of their respective response ratios (Darling and Côté 2008). Then, we compared the observed mean response ratio from the combined factors to the expected additive response ratio. If the observed response ratio from the combined factors fell below or above the 95% confidence limits of the additive response ratio, the effects were classified as non-additive that either increased or decreased the expected cumulative negative impact on seed dispersal, respectively. Conversely, if the response ratio from the combined factors overlapped with the predicted additive 95% confidence limit, the experiment was classified as additive.

Results

Baseline scenario

Over the 25-yr simulated period, both frugivorous mammals dispersed large numbers of *P. bourgaeana* seeds across the target landscape (Fig. 1B), with foxes dispersing about half as many as badgers (8881.8 ± 596.7 and $16\,003 \pm 833.2$ [mean \pm 1 SD], respectively). Furthermore, there were marked differences between disperser species in the proportion of dispersal events across different habitat types (Fig. 1C–D). For instance, whereas the number of seed dispersal events by badger in the Mediterranean scrubland was about 2.3 times larger than that by fox, the numbers of fox dispersal events into both oldfields and marshes (i.e. sink habitat to *P. bourgaeana*) was 1.4-fold larger than that of badgers (Fig. 1C–D). Foxes delivered similar numbers, and badgers much lower numbers, of seeds into 'other habitats' (Fig. 1C–D).

Effects of defaunation and density compensation on overall and habitat-specific seed dispersal

Overall, *P. bourgaeana* dispersal events in the system gradually declined (compared to the baseline value) 15, 29 and

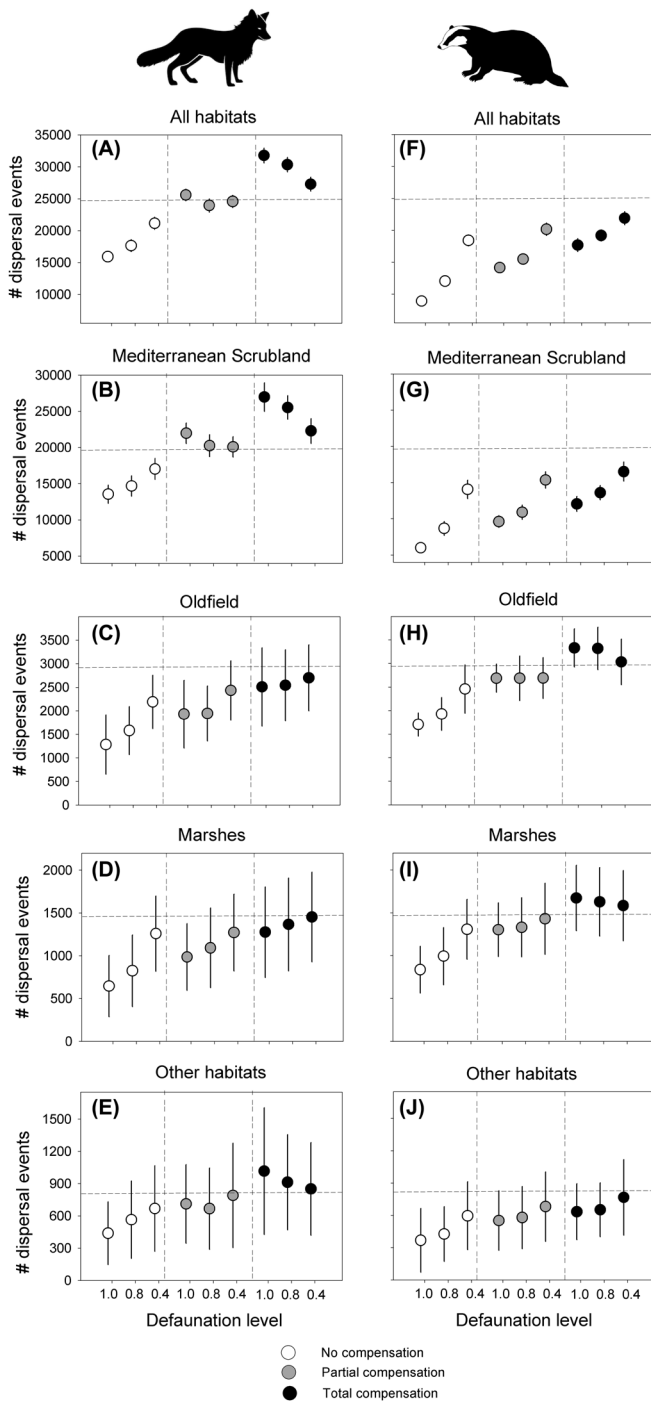


Figure 2. Overall and habitat-specific impact of red fox (A–E) and badger (F–J) defaunation and density compensation on seed dispersal quantity (mean \pm 1 SE) under a scenario of baseline tree mortality (100 simulations per treatment combination). The dashed horizontal lines represent the baseline values under scenarios of no defaunation. The dashed vertical lines separate scenarios of density compensation.

36% under scenarios of mild, intermediate and complete fox defaunation, respectively (Fig. 2A, 3A, E). The impact of fox losses on seed dispersal varied among habitat types, being

greatest in oldfields and marshes (24–58% and 16–57%, respectively; Fig. 2C–D). When fox losses were compensated with increases in badger numbers, either partially or totally, the overall number of *P. bourgaeana* dispersal events reached or even overreached the baseline value, respectively (Fig. 2A–E, 3A versus B, E versus F).

As predicted, the extent to which compensation by badgers for reduced fox numbers led to a recovery on seed dispersal was dependent not only on compensation level but also on habitat type. For instance, when fox losses were totally compensated with increased badger numbers, seed dispersal into Mediterranean scrubland exceeded the value observed in the no-defaunation scenario by up to 37% (Fig. 2B). Conversely, seed dispersal into oldfields or marshes was not fully recovered when fox losses totally compensated with increased badger numbers (Fig. 2C–D). Finally, compensation with badgers augmented the number of dispersal events into ‘other habitats’, reaching the baseline levels (Fig. 2E).

Badger losses had an overall stronger impact on *P. bourgaeana* seed dispersal than did fox losses. Complete badger defaunation reduced the total number of dispersal events by 64% relative to the baseline value (Fig. 2F, 3M versus 1C). The effect of badger losses on seed dispersal was also habitat-specific, being particularly marked for the Mediterranean scrubland (29–70%; Fig. 2G). Furthermore, when badger losses were compensated by increases in fox numbers, the overall number of seed dispersal events never reached the baseline value (Fig. 2F). The extent to which compensation with red foxes led to a recovery on *P. bourgaeana* seed dispersal was highly dependent on compensation level and habitat type (Fig. 3I–P). Compensation with foxes increased seed dispersal into the Mediterranean scrubland, though never led to a level close to the baseline value (Fig. 2G). Compensation with foxes markedly increased the number of seed dispersal events into both the oldfield, marshes and ‘other habitats’, almost reaching or overreaching the baseline values (Fig. 2H–J).

Combined effects of increased tree mortality and defaunation on the overall and the habitat-specific seed dispersal

Increased tree mortality led to an overall decline in seed deposition of 17%, with a rather constant impact across habitat types (i.e. ranging 17–19%; see Supplementary material Appendix 4). Such a decrease in seed dispersal resulting from increased tree mortality was small compared to the 49% decrease found in fruit production (Supplementary material Appendix 4). When both increased tree mortality and fox losses acted simultaneously, the overall number of seed dispersal events declined 29–46% (depending on defaunation level) compared to the baseline (Fig. 3C, G versus 1D, 4A). The magnitude of the combined effect of fox losses and increased tree mortality on seed dispersal varied noticeably across habitat types, with a trend toward greater effect in the oldfields and the Mediterranean scrubland as compared with marshes and ‘other habitats’ (Fig. 4B–E). On the other

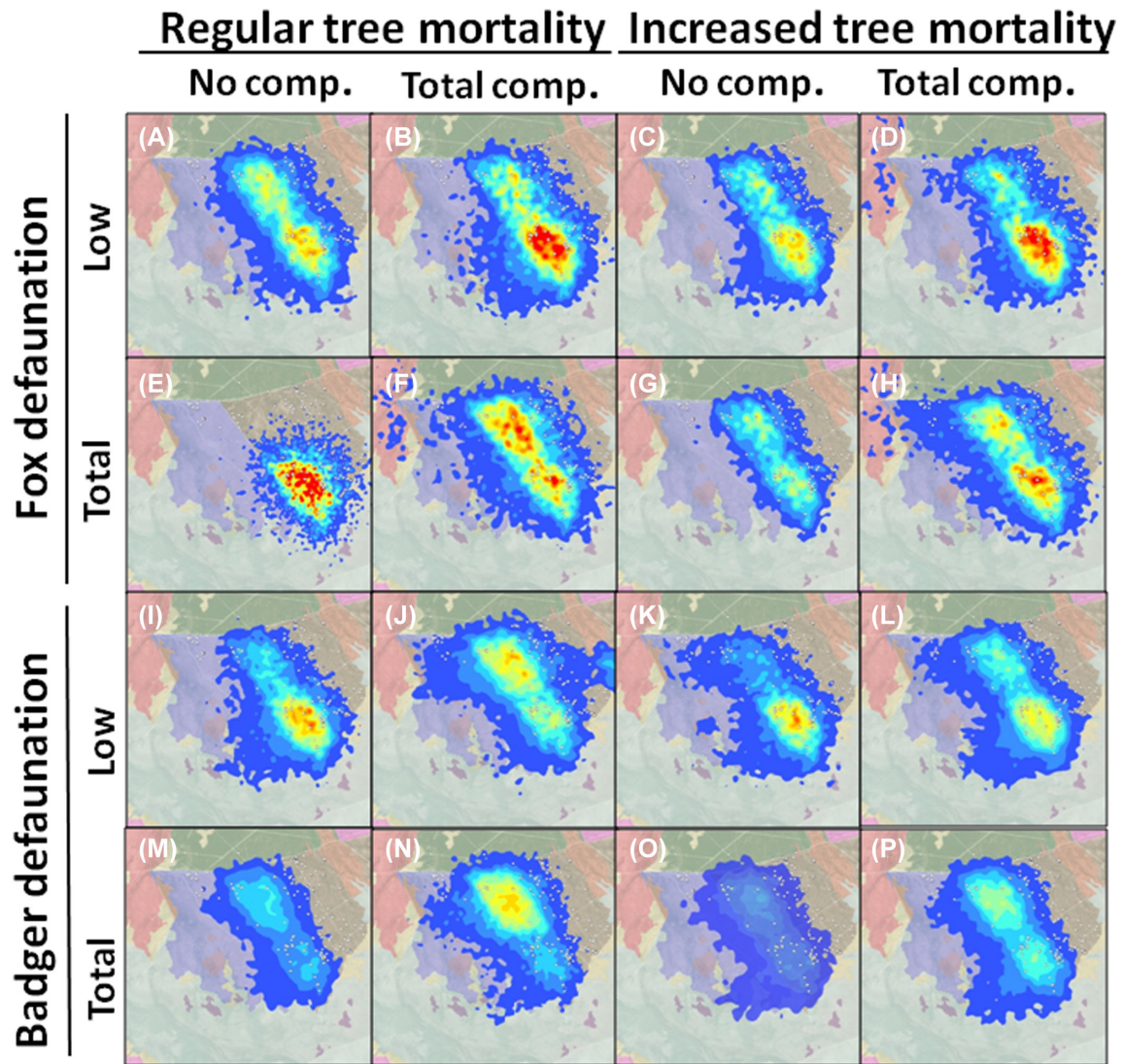


Figure 3. Seed rain under different scenarios of low and complete red fox (A–H) and Eurasian badger (I–P) defaunation. Each defaunation scenario is shown for different combinations of tree mortality (baseline versus increased) and density compensation (total versus no compensation) with badgers or foxes. Other conventions as in Fig. 1.

hand, although compensation with badgers increased the overall number of dispersal events, this increase was often insufficient to offset the combined impact of both stressors on seed dispersal (Fig. 4B–E). Finally, the combined effect of increased *P. bourgaeana* mortality and fox losses on seed dispersal was less severe than the expected additive effect for the scenario of complete defaunation (Fig. 5A).

The joint effect of increased *P. bourgaeana* mortality and badger losses substantially reduced the overall number of seed dispersal events (39–71%; Fig. 4F). Further, their joint effect on seed dispersal varied largely in magnitude across habitat types, being particularly strong in the Mediterranean scrubland and the oldfields (Fig. 4G–H). On the other hand, while compensation with foxes increased the overall number of seed dispersal events, it was generally insufficient to offset

the impact of both stressors (Fig. 4F–JB, Fig. 3L, P). As with fox defaunation, the joint effect of increased *P. bourgaeana* mortality and badger losses was less severe than the expected additive effects for the scenarios of intermediate and complete defaunation (Fig. 5B).

Discussion

Although defaunation is known to limit seed dispersal (Galetti et al. 2013, Bello et al. 2015, Donoso et al. 2017) little is known concerning the spatial structure of this reduction (Anderson et al. 2011) and the extent to which density compensation could ameliorate it (Cordeiro and Howe 2003, Fricke et al. 2018). Additionally, it remains

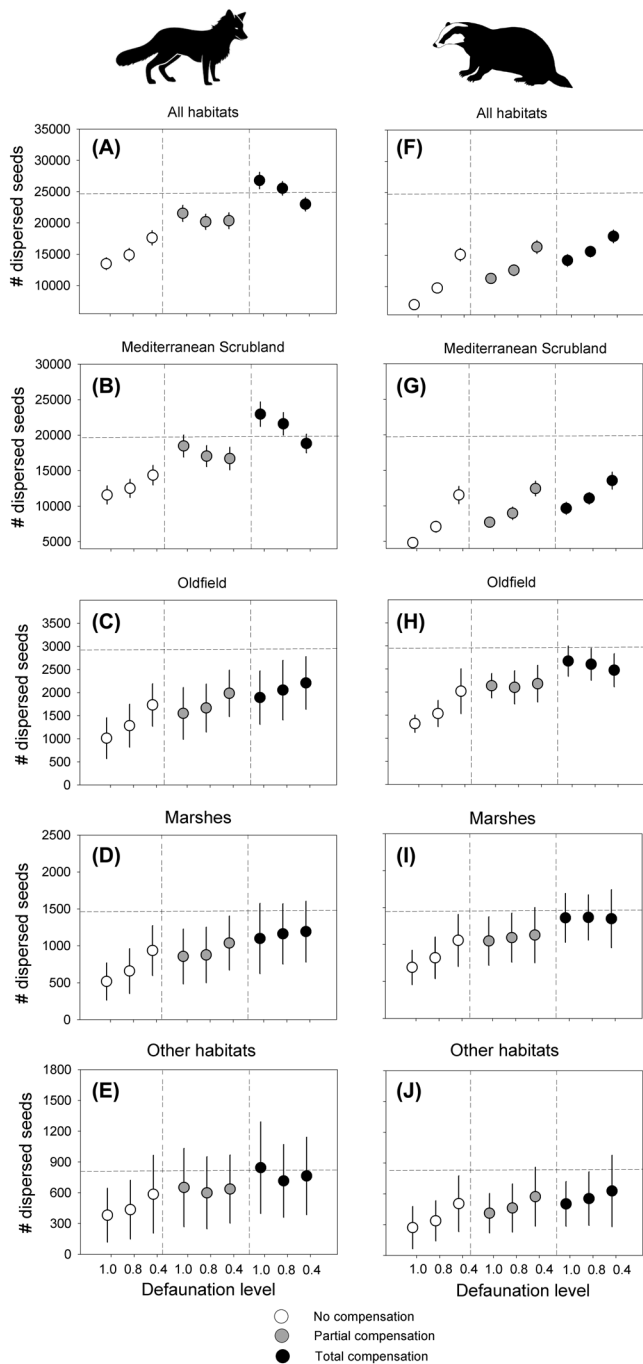


Figure 4. Overall and habitat-specific impact of red fox (A–E) and badger (F–J) defaunation and density compensation on seed dispersal quantity (mean \pm 1 SE) under a scenario of increased tree mortality (100 simulations per treatment combination). The dashed horizontal lines represent the baseline values under scenarios of no defaunation. The dashed vertical lines separate scenarios of density compensation.

unclear how other global change components, such as increased tree mortality, interact with defaunation to influence ecosystem services. Our individual-based model allowed us to quantitatively investigate the combined

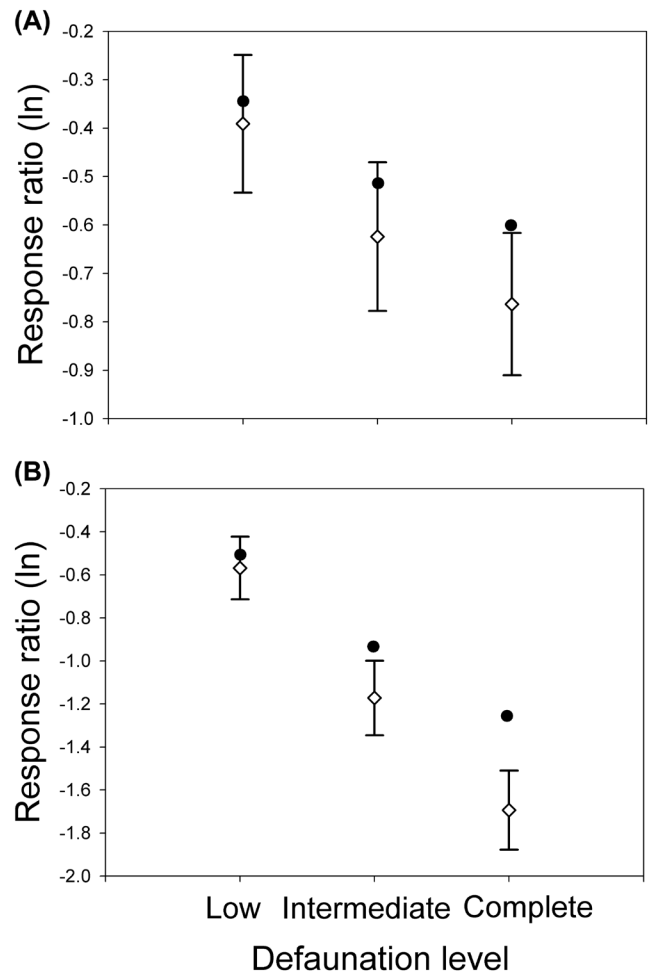


Figure 5. Comparison of the observed mean response ratio from scenarios where defaunation and increased tree mortality acted in combination (black circles) to the expected additive response ratio based on the sum of the individual effects of defaunation and increased tree mortality (vertical bars). Scenarios of low, intermediate and complete red fox (A) and badger defaunation (B) were simulated. Note how the observed response ratio from the combined factors was often less negative (i.e. less strong) than the upper 95% confidence limits of the additive response (vertical bars) indicating that defaunation and increased tree mortality lead to non-additive effects that ameliorated the impact on seed dispersal.

effects of defaunation and increased tree mortality on seed dispersal in a highly heterogeneous landscape. We found that 1) these two stressors markedly limited not only the quantity of *P. bourgaeana* seed dispersal (sensu Schupp et al. 2017) but also its quality, since the impact on seed dispersal strongly varied among habitats differing in suitability for subsequent seed and seedling survival; 2) density compensation generally has a marked positive effect on seed dispersal although this was generally reduced under scenarios of increased tree mortality; and 3) defaunation and increased tree mortality did not necessarily operate in an additive fashion, highlighting the importance of investigating the joint impact of different

global change components on ecosystem functioning (Paine et al. 1998, Reich et al. 2006, Darling and Côté 2008, Galic et al. 2018).

The effects of defaunation and density compensation on seed dispersal

The effect of defaunation on seed dispersal was strong for both disperser species, though badger losses had a stronger impact. This pattern likely relates to badgers being more frugivorous and dispersing more *P. bourgaeana* seeds than foxes (Fedriani et al. 1998, 1999). Nonetheless, the impact of defaunation on seed rain was markedly disperser species- and habitat-specific. For instance, under complete fox defaunation, the strongest reduction of seed dispersal took place in the marshes and the oldfield, which received half as many seeds as under baseline conditions. Under complete badger defaunation, however, the reduction in seed dispersal was particularly strong in the Mediterranean scrubland, reaching only 30% of the baseline value. These differences relate primarily to the contrasting habitat use, movements and seed retention times by foxes and badgers in Doñana (Fedriani et al. 2018) which are difficult to quantify without use of a model that puts all information into a common framework. However, the loss of either disperser species had strong impacts on seed dispersal into the Mediterranean scrubland because both species use the scrubland intensively (especially during daytime), and this is where most *P. bourgaeana* trees are located. Overall, these results indicate that relatively slight behavioural differences of seed dispersers species, which a priori could be judged rather functionally redundant (Zamora 2000, García et al. 2014), lead to substantial functional differences crucial to properly predict the impact of defaunation on ecosystem functioning.

Evidence for the density-compensation hypothesis for seed-disperser systems is often contradictory (Cordeiro and Howe 2003, Donatti et al. 2009, Bueno et al. 2013, Fricke et al. 2018). Our results indicate that, despite certain functional differences between frugivorous foxes and badgers, density compensation might ameliorate the impact of defaunation on seed dispersal, albeit to a variable extent. For instance, when fox losses were completely compensated with badgers, seed dispersal into Mediterranean scrubland increased to a level that even surpassed the baseline scenario. Similar compensation has been documented not only among native seed dispersers (Cordeiro and Howe 2003, Zhou et al. 2013) but also by introduced and domestic species (García et al. 2014, Cares et al. 2018, Muñoz-Gallego et al. 2019). However, such apparent compensation could be less complete if disperser species differ in subtle but key aspects of the seed dispersal process (e.g. microhabitats of deposition or dispersal distances; Jordano et al. 2007, García-Cervigón et al. 2018). At the plant community level, given the differential habitat requirements by plant species and the differential habitat use by seed dispersers, the potential for density compensation is likely to be more variable and difficult to predict (Donoso et al. 2017, Morán-López et al. 2020).

Importantly, the reported changes in habitat-specific seed dispersal due to defaunation and density compensation have critical demographic consequences for the target tree population. For example, because the oldfields are mostly vacant but suitable habitats, a decrease in *P. bourgaeana* seed dispersal into this habitat due to fox losses would reduce the potential of this tree species to expand beyond its current distribution (Fedriani et al. 2018). Conversely, since the scrubland is a habitat already colonized by *P. bourgaeana*, a decrease in seed dispersal into this habitat due to badger losses would mostly impact the local tree population persistence (Jordano 2017). Finally, the reduction of seed dispersal into the marshes due to disperser losses does not negatively impact the tree dynamics, as this habitat is unsuitable for the tree recruitment and establishment and thus represents a population sink (Anderson et al. 2011, Spiegel and Nathan 2012, Ehrlén and Morris 2015). As a whole, these results emphasize the importance of considering changes in habitat-specific seed dispersal when assessing the effects of different global change components on seed dispersal across heterogeneous landscapes.

Joint effect of increased tree mortality and defaunation on seed dispersal

Understanding the potential mechanisms leading to non-additive effects is essential to predict the outcomes of global change on ecosystem functions (Didham et al. 2007, Côté et al. 2016). Our simulations revealed that the effects of increased tree mortality and defaunation interacted in non-additive ways. Both stressors could interact in reducing the seed dispersal service if, for example, under low tree density seed dispersers were disproportionately less efficient in foraging fruits (and thus dispersing seeds) than under baseline tree densities. Interestingly, we revealed that the combined effect of both stressors was often smaller than the sum of their isolated effects (Darling and Côté 2008). A plausible mechanism explaining such non-additivity is that, under scenarios of complete defaunation the per capita availability of fruits for seed dispersers was higher. This partially ameliorated the effect of increased tree mortality, which decreased fruit availability. In other words, under scenarios of complete defaunation and increased tree mortality depletion of the few available fruit patches occur less often (or more slowly) than under high abundance of seed dispersers (i.e. no defaunation). This type of interaction between both environmental stressors reduces the cumulative impact on ecosystem function (i.e. seed dispersal) in contrast to synergistic interactions or additive effects (see also Côté et al. 2016). Therefore, from a conservation perspective, our results may provide support for cautious optimism (Didham et al. 2007, Brook et al. 2008, Darling and Côté 2008).

The potential for density compensation to ameliorate the impact of defaunation on seed dispersal was strongly reduced under increased tree mortality. This likely is related to a reduction of the per capita availability of fruits for seed dispersers under density-compensation (more animals) and increased tree mortality (fewer fruits). This

unpredicted pattern was particularly marked for the joint effect of badger losses and increased tree mortality, where density compensation seldom led to dispersal rates reaching the baseline value. It is worth noting the possibility that during periods of increased tree mortality (i.e. lower fruit availability) foxes and badgers shift their foraging towards other, more abundant, food types (Fedriani et al. 1999). In such a scenario, which merits further research, the detrimental effect of increased tree mortality on seed dispersal would be even higher than that predicted by our simulations. Of concern, anthropogenic landscapes commonly experience multiple stressors, including both defaunation and increased tree mortality, due to human activities such as hunting, logging and pest introductions (Lewis et al. 2015, Trumbore et al. 2015). That is the case, for example, of large areas of Borneo, Congo and Amazonia where intensive logging and defaunation co-occur and largely hamper ecosystem functioning and resilience (Lewis et al. 2015). Thus, investigating the joint impact of contrasting perturbations in these areas is imperative to accurately predict changes on ecosystem functioning.

To conclude, our simulation study reveals that defaunation may have a strong impact on the seed dispersal quantity and quality of a large-fruited tree, and this impact is likely to vary noticeably across the landscape. The effect of ongoing defaunation is particularly critical for plants dispersed by large and medium-sized vertebrates, especially in areas that have been historically defaunated (Terborgh et al. 2001, Fedriani et al. 2010, Pires et al. 2018), and it is likely exacerbated in areas with high anthropogenic impacts, as these frequently are characterized by intense tree mortality. In these systems, the extant seed disperser species are limited and thus less likely to fully replace the functions of other missing species. Understanding whether and how the joint effect of global change components on seed dispersal scale up to the community and ecosystem levels (Terborgh et al. 2001, Perino et al. 2019), and how prevalent are non-additive interactions between them, remains an important challenge for ecologists and conservation biologists. Our results strongly support the critical importance of biodiversity and mutualistic interactions for the emergence and maintenance of ecosystem functions as well as the services that they support (Oliver et al. 2015, Schleuning et al. 2015).

Data availability statement

Data available from Figshare Digital Repository: <<https://doi.org/10.6084/m9.figshare.12318710.v1>> (Fedriani et al. 2020).

Acknowledgement – The laboratory of GIS and Remote Sensing (LAST, EBD), in particular, Isabel Afán and David Aragonés, provided essential assistance. Douglas Kelt and two anonymous reviewers provided numerous helpful comments to earlier draft that improved the content and presentation of this study.

Funding – Funding received from Spanish Ministry of Science, Education and Universities, PGC2018-094808-B-I00. DA by

the Spanish Ministry of Economy, Industry and Competitiveness through the research project CGL2017-84269-P and TW by the ERC advanced grant 233066.

Author contributions – JMF, DA, TW, VG conceived the ideas and developed the model. JMF, DA analyzed the data. JMF run this long-term project, gathered essential field-data and wrote the first draft. All authors significantly contributed to the final manuscript.

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Supplementary material (available online as Appendix ecog-05047 at <www.ecography.org/appendix/ecog-05047>). Appendix 1–4.