Seed dispersal by changing frugivore assemblages: a mechanistic test of global change effects

Javier Rodríguez-Pérez, Daniel García, Daniel Martínez and Juan Manuel Morales

J. Rodríguez-Pérez (http://orcid.org/0000-0002-1292-9090)(jvr.rodriguez@gmail.com), D. García and D. Martínez, Depto Biología de Organismos y Sistemas, Univ. de Oviedo, and Unidad Mixta de Investigación en Biodiversidad (UMIB, CSIC-Uo-PA), ES-33071 Oviedo, Spain. Present address for JRP: Aranzadi Sciences Society, Zorroagagaina 11, ES-20014, Donostia-San Sebastián, Spain. – J. M. Morales, Laboratorio Ecotono, INIBIOMA-CONICET, Univ. Nacional del Comahue, Bariloche, Argentina.

In the face of global change it is important to understand how changes in species abundance and richness can affect ecosystem functions. Here we modelled seed dispersal by animals in a fragmented secondary forest of the Cantabrian Range (northwestern Iberian Peninsula), simulating the activity of six frugivorous bird species when dispersing three species of fleshy-fruited trees. We calculated the density and richness of seeds deposited across a forested landscape, as well as the density of seeds arriving to open areas. We 1) study the complementarity of functional traits of each species with frugivore assemblages varying in species compositions (i.e. abundance and richness of bird assemblages), 2) identify those bird species whose functional roles are not redundant, and 3) explore the response of seed dispersal to random losses and to two non-random bird loss scenarios (i.e. overhunting and fewer individuals from migrant species). We found that simulations with the avian composition observed in the field (i.e. with uneven abundances of six bird species) led to values of seed dispersal higher to those emerging from four bird species equally abundant. The selective removal of dominant bird species led to significant decays in seed dispersal, suggesting non-redundant roles of abundant bird species. Seed dispersal decays were stronger under non-random than random scenarios of bird loss. In terms of seed density, the functional decays also differed between the scenarios of overhunting and reduced arrival of migrant birds, notably beyond 50% changes in bird species composition. Our results illustrate the need to integrate species composition (controlling for bird abundance and richness) and their sensitivity to disturbances when predicting the impact of global change on ecosystem functions.

The decline of ecological functions resulting from global change depends on how extinction drivers alter species communities (Duffy 2003, Elmqvist et al. 2003). The magnitude and the stability of ecosystem functions depend not only on the composition of biotic communities, as species may differ in their abundance, and in morphological and behavioural traits (Wardle et al. 2011, Luck et al. 2012), but also on the interactions between species (Naeem and Wright 2003, Balvanera et al. 2006, Schleuning et al. 2015). On one hand, complementarity in species traits and interactions within communities leads to an increased magnitude of ecosystem functions (Díaz et al. 2013, Schleuning et al. 2015). On the other hand, given that species vary in their susceptibility to disturbance, losses of species with singular traits may produce large changes in ecosystem functions. Conversely, species with common traits may provide stability to ecosystem functions due to redundancy and thus, the loss of one of these species would not lead to strong ecological disruptions. Likewise, non-random species losses have greater impacts on ecosystem stability compared to random losses, meaning that the identity and the order of species extinctions may jeopardize ecological functions (Gross and Cardinale 2005, McIntyre et al. 2007). Therefore, predicting changes in an ecosystem under specific drivers of global change requires not only forecasting of the variations in functional mechanisms surrogate to a given species composition, but also understanding how the alteration of species assemblages compromise stability and resilience to particular ecosystem functions (Larsen et al. 2005, Hillebrand and Matthiessen 2009).

The seed dispersal function provided by frugivorous animals is a key process affecting the abundance and distribution of endozoochorous plants (Levine and Murrell 2003, Robledo-Arnuncio et al. 2014). In plant–frugivore systems, the complex interplay between the abundance, behaviour and activity of frugivores and resource availability at different spatial scales, from microhabitat to landscape, together with disturbances can affect the seed dispersal function (Côrtes and Uriarte 2013). It is important that such interplay defines the functional particularities of frugivore species that are relevant for the growth of plant populations, the maintenance of plant diversity, and the colonization of new habitats (Robledo-Arnuncio et al. 2014). It is well known that anthropogenic disturbances can cause frugivore losses and hamper plant regeneration, but it is difficult to predict the impact that disturbances might have on the

seed dispersal function (McConkey et al. 2011, Farwig and Berens 2012). Studies incorporating functional trait variability among frugivores explicitly and their sensitivity to disturbances are still rare but are essential for predicting how animal-dispersed plant populations will respond to global change (Mokany et al. 2014). Hence, we need to integrate different scales of organization (i.e. from individuals to species assemblages) governing frugivory and seed deposition, with the aim of predicting the effects of global-change drivers on plant populations (Côrtes and Uriarte 2013, Farwig and Berens 2012, Robledo-Arnuncio et al. 2014).

Here, we explored the relationship between the composition of a frugivore assemblage (in terms of the relative abundances and the richness of frugivore species) and the seed dispersal function derived from frugivore activity, and assessed the response of seed dispersal to random and non-random losses of frugivores. We focused on a study system composed of six frugivorous birds (thrushes) and three fleshy-fruited trees from the fragmented forests of the Cantabrian Range (northwestern Iberian Peninsula). We followed a mechanistic approach based on field observations of the abundance, richness, behaviour, spatially-explicit activity while foraging, and habitat preferences of thrushes (Martínez et al. 2008, García et al. 2013, Morales et al. 2013). Given that we can simulate the mechanisms underpinning the variability in the seed dispersal function, we explored three issues critical for assessing how frugivore losses could affect the seed dispersal. Firstly, seed dispersal function depends on the complementarity of functional traits of each species and we thus ran simulations controlling for bird abundance and richness within different frugivore assemblages to study their functional outcomes. Secondly, seed dispersal varies with frugivore species and we thus simulated losses of single species to identify bird species whose functional roles are not shared by the rest of the assemblage. And thirdly, along gradients of frugivore losses we tested the resilience of the seed dispersal function; for this purpose we simulated random and non-random scenarios of bird loss based on the species-based sensitivity to global change.

Material and methods

Study system

We studied the plant–frugivore assemblage of birds and fleshy-fruited trees in secondary forest in the Cantabrian Range (northwestern Iberian Peninsula). This forest is highly fragmented and dominated by fleshy-fruited trees, mostly holly *Ilex aquifolium*, hawthorn *Crataegus monogyna* and yew *Taxus baccata*, whose fruits ripen in autumn (September to November). These trees are mainly dispersed by six species of thrush *Turdus* spp., of which blackbird *Turdus merula*, mistle thrush *T. viscivorus* and song thrush *T. philomelos* are residents although their numbers are swelled in winter by northern European migrants moving from their breeding to their winter quarters. The fourth species, ring-ouzel *T. torquatus*, migrates from northern Europe in our study site and could only be seen during autumn. By contrast, fieldfare *T. pilaris* and redwing *T. iliacus* are strictly over-wintering species and they can be frequently seen during the winter period in the

northern Iberian peninsula (Tellería and Santos 1982). In our study site, *T. merula*, *T. viscivorus*, *T. philomelos* and *T. iliacus* comprise more than 90% of bird sightings (Martínez et al. 2008). Also, *T. viscivorus*, *T. pilaris*, *T. iliacus* and *T. torquatus* are flocking species, whereas *T. merula* and *T. philomelos* are less gregarious (Martínez et al. 2008). The other species that interact with fleshy-fruited trees are either seed predators (e.g. rodents; García et al. 2005a) or occasional dispersers (i.e. carnivorous mammals; Martínez et al. 2008, Peredo et al. 2013). Thrushes in the Cantabrian forest generate species-specific spatial patterns of seed dispersal (Morales et al. 2013), affecting tree recruitment (García et al. 2005b), and triggering the recolonization of deforested areas (García et al. 2013). Overall, bird richness affects the quantity and, particularly, the quality of seed dispersal (García and Martínez 2012).

Study site and field data

The study site was located in the Sierra de Peña Mayor (900 m a.s.l., Asturias region, Spain; Fig. 1), a mountain range where secondary forest is intermingled with meadows, heathland and limestone rocky outcrops. For details about field data collection see Supplementary material Appendix 1. We set up a 400 × 440 m (17.6 ha) rectangular plot where there is a gradient of forest loss from the northeast to the southwest (Fig. 1). Environmental variables were sampled in a grid of 440 20 × 20 m cells (Fig. 1). We developed a geographical information system (GIS, ArcGIS ver. 9.0), which incorporated the grid and a layer of digitized forest cover (to estimate the percentage of forest cover per cell). During the 2009 fruiting season, we visually sampled the fruit crop of individual fleshy-fruited trees by means of a semi-quantitative fruiting abundance index (FAI; Saracco et al. 2004); in that year, *C. monogyna* produced 8.53% of the total fruit crop, *I. aquifolium* 83.92% and *T. baccata* 7.55%. We also performed direct observations of birds in our study plot to estimate their richness and abundance (García et al. 2013); in 2009, direct observations showed that 49.1% birds were *T. iliacus*, 20.7% *T. merula*, 17.2% *T. viscivorus*, 10.5% *T. philomelos*, 1.6% *T. pilaris* and 1.0% *T. torquatus*. We also recorded bird activity and foraging movements (i.e. flight distances, perching microhabitat and number of fruits consumed) over observation sequences from 2007 to 2009 (Morales et al. 2013). Finally, we monitored seed dispersal by collecting seeds deposited in bird faeces in sampling stations distributed across the whole landscape (García and Martínez 2012).

Mechanistic model of seed dispersal

We predicted seed deposition by means of event-driven stochastic simulations, based on the interplay between spatially-explicit habitat features and the activity of thrushes (Morales et al. 2013). We modified the model of Morales et al. (2013) to evaluate questions related to species-specific complementarity in functional traits affecting seed dispersal, to identify key species whose functional roles are not shared by other species, and to explore the effect of bird losses on seed dispersal. In essence, our model captures the rules of foraging movements and activity of birds based on the observed bird
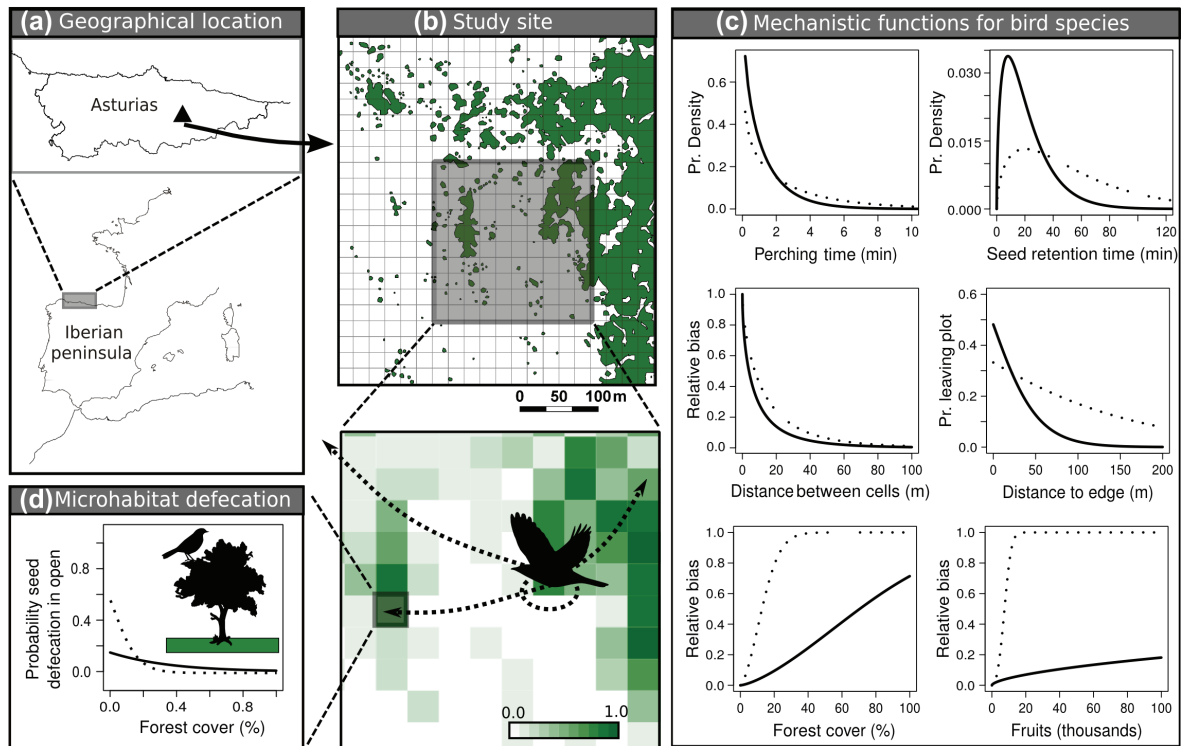
Figure 1. Geographical location (a) and details of the study site (b), functions describing bird activity while foraging within the study plot (c), and details of microhabitat deposition (open versus forest) of simulated birds (d). For the study site (b), we show forest cover (green) and the subdivision of the plot into cells (upper panel; for further details see Supplementary material Appendix 1). In a detailed area of the study site (lower panel), we plotted the proportion of forest cover per cell (green hues), and an example of simulated bird activity while foraging (arrows represent likely movements within the landscape). The functions fitted to bird species (c) are shown; for the sake of clarity we only present the functions corresponding to two bird species (e.g. *T. iliacus* in solid line and *T. visvivorus* in dotted line; Morales et al. 2013). Finally, we present the functions describing microhabitat seed deposition for *T. iliacus* and *T. viscivorus* (d; for details, Supplementary material Appendix 2).

tracks (Supplementary material Appendix 1). These behavioural rules depend on habitat attractiveness as perceived by birds, and were fitted to each of the six species of thrushes (Fig. 1; Morales et al. 2013).

Common features of the current model and the model of Morales et al. (2013) are that: 1) bird perching time is independent of fruit consumption; 2) gut retention time of ingested seeds is parameterized for each bird species; 3) fruit consumption depends on both per-cell fruit availability and observed fruit consumption rates; 4) birds fly at a constant speed of 6 m s⁻¹, following a straight line to and from landscape cells; 5) bird foraging movements depend on the distance from the current location to the destination cell, the proportion of forest cover, the number of fruits at the destination cell; 6) the probability of a bird leaving the simulation area depends on the distance to the nearest plot border (birds are allowed movement until they depart from the simulated landscape). Every time a simulated bird arrives at a landscape cell, spends an amount of time perching (drawn from a gamma distribution fitted to observations from each species) and consumes fruits (drawn from a zero-inflated Poisson distribution) depending on the abundance of fruits of the different tree species in the cell (i.e. birds do not have built-in preferences for fruit species). Once frugivory occurs, ingested seeds spend some time inside the bird (i.e. gut-passage time drawn from a gamma distribution) before

being dropped. When the perching time expires, the simulated bird makes another move and can stay in the same landscape cell, move to another one or leave the simulated area. For parameterizations of mechanistic functions fitted for the different bird species see Fig. 1c.

In the current model version, we implemented two additional features. First, we included the number of seeds of each fleshy-fruited species per bird dropping based on field data (Martínez et al. 2008). For each track, a simulated bird defecates monospecific seed clumps (87.6% of the examined droppings included only one species; Martínez et al. 2008), with a number of seeds drawn from a Poisson distribution with parameters depending on each fleshy-fruited species (Martínez et al. 2008). Second, we incorporated the fine-scale features of the seed deposition microhabitat within the landscape cells, which depended on bird species' probability of perching in a tree or landing on open ground (Supplementary material Appendix 1 Fig. A3). For each track, the probability of seed defecation of simulated bird in (a) tree covered versus (b) open microhabitat (i.e. drawn from a logistic distribution) depended on the proportion of forest cover per each cell and the species-based probability to perch in trees. For methodological details and microhabitat parameterizations see Supplementary material Appendix 2.

Our model thus allows predictions of seed dispersal patterns which emerge from the interaction between

abundance and behaviour of bird species with the distribution and availability of fleshy-fruited trees in the 440 cells of the simulated landscape (Fig. 1). The relative abundance of simulated bird species derives from observed abundance in our study plot in 2009 (Supplementary material Appendix 1). For each seed dispersal event, the model provides 1) the identity of the mother plant, 2) the identity of the bird, 3) the cell-referenced spatial position, and 4) the microhabitat where seeds were deposited (forest versus open microhabitats). Finally, we constructed simulated maps of the abundance of each of the six thrush species and the number of seeds of each of three tree species deposited by birds in different microhabitats.

Summary statistics of simulated seed rain and their validation

For each simulation, we calculated several summary statistics (i.e. seed dispersal components, hereafter) representing the quantity and quality of seed dispersal across the whole landscape: 1) seed density (the total number of seeds deposited per cell), 2) seed species richness (the number of seed species deposited per cell), and 3) seed density in open areas the number of seeds defecated in open microhabitat per cell, divided by the proportion of open microhabitat in that cell). All these values were calculated for each 20×20 m cell of the landscape, and then averaged over four adjacent cells resulting in 110 40×40 m blocks (landscape sampling cells for seed dispersal). This aggregation sought to make the results of the simulation study comparable (and able to be validated, see below) to those in the observational study by García and Martínez (2012) (see Supplementary material Appendix 1 for sampling design).

To test the validity of our model predictions, we simulated 500 bird tracks in our grid-based landscape (Fig. 1), using the relative abundance and richness of birds observed during 2009. For each simulation we calculated the three seed dispersal components, and compared them to those calculated from field data; this procedure was repeated 30 times. The generalized coefficient of determination (adjusted R^2) between observed and simulated values measured the amount of observed variation explained by simulations, whereas a partial Mantel-r test between observed and simulated data estimated the degree of spatial concordance between the distributions of observed and simulated data. We found that our mechanistic model was able to explain a good amount of observed variation in seed density ($R^2 = 0.545$) and seed richness ($R^2 = 0.544$), whereas for seed density in open microhabitats our model explained a small fraction of the variability in the data ($R^2 = 0.166$). We also found a good spatial concordance between observed and simulated values (i.e. Mantel-r = 0.450 for seed density, 0.490 for seed richness and 0.429 for seed density in open microhabitats). For further details see Supplementary material Appendix 3.

Effects of bird abundance and richness on seed dispersal

We sought to explore the effect of the composition of the frugivore assemblage on seed dispersal, and we thus performed simulation experiments with different combinations of species abundances and richness. We performed simulations mimicking the relative abundance and richness observed under real-world conditions (i.e. 'observed bird composition' hereafter), based on field observations in 2009. The resulting seed dispersal patterns were then compared to those produced by different combinations of bird abundance and richness. To isolate the relative effect of species richness from that of species abundance, we assumed density-dependent compensation between bird species (i.e. the decrease of population size of a given species is compensated with the increase of another, and vice versa). For each scenario we obtained 30 replicate runs, simulating a constant number of bird tracks in each run and estimating the values of the seed dispersal components in each of the 110 40×40 m blocks (Supplementary material Appendix 1); this time we simulated 1000 tracks per run to have sufficient number of seeds dispersed by the less abundant bird species.

A first set of simulations sought to explore the effect of bird richness on seed dispersal components, and thus the effect of bird composition on seed dispersal only depended on species richness and not on the number of individual birds (i.e. pure richness bird compositions, hereafter). Later simulations were conducted with even abundances of bird species, at combinations of increasing bird richness; in other words, we simulated pure richness bird compositions varying from one to six bird species. Simulations with pure richness bird compositions were compared with that observed, with the aim to test how varying combinations of bird abundance and richness affect seed dispersal.

In addition, we tested the contribution of each bird species to seed dispersal by simulating bird extinctions to identify those species whose functional roles were unique. Hence, we removed one bird species from the original six (i.e. poorer bird compositions, hereafter), and we repeated this procedure with each of the six frugivore species. In addition, we simulated single-species losses with the observed and the pure richness bird compositions, and compared these with the observed composition of six bird species. For each seed dispersal component, we computed a 'component bias' as the percentage of values above and below the 1:1 line relating observed and poorer bird compositions (i.e. values close to zero mean no change comparing poorer and observed bird compositions).

Seed dispersal in scenarios of bird loss

We ran simulations to test how seed dispersal may respond to bird losses related to potential global change alterations. In these simulations we explored how properties of seed dispersal changed along gradients of decreasing abundance of bird species affected by different disturbance types. We considered a scenario of 'random' bird losses, and two scenarios of 'non-random' losses based on the extinction drivers potentially operating in our study system: over-exploitation by hunting and loss of migrant individuals due to climate change. First, in the 'random loss' scenario bird losses only depended on a sampling effect. We generated a gradient of bird loss by removing individual birds, and thus the most abundant species would be the most resilient to extinction. Second, in the scenario of 'loss of species

by overhunting', game species were those suffering losses, mimicking a situation of increased hunting pressure. We thus reduced the abundance of four game species of thrushes (namely, *T. iliacus*, *T. viscivorus*, *T. philomelos* and *T. pilaris*), while maintaining others constant. Third, in a scenario of 'loss of migrant species' migratory birds had lower arrival rates, and we thus simulated loss of migrant individuals. In this scenarios there are decreases in the abundance of *T. iliacus*, *T. torquatus*, *T. pilaris*, *T. viscivorus* and *T. merula*. For further details about scenarios see Supplementary material Appendix 4.

As a baseline we started with scenarios matching the observed bird composition recorded in 2009, and we subsequently decreased the abundance of the different bird species (Fig. 2) depending on specific sensitivities to disturbances (Supplementary material Appendix 4). For the simulated scenario of a given disturbance, we altered bird composition based on a reduction in the relative abundance of those species affected by that disturbance. We drop a random number from 1 to 75% of alteration as we assumed that species did not go completely extinct in all scenarios); we repeated latter procedure 50 times simulating a constant number of 1000 bird tracks in each run. For each scenario of bird loss, the values of the seed dispersal components with decreasing bird relative abundance were calculated across the whole landscape as well as the average of all blocks in our landscape. In later simulation

experiments we assumed that the decline in abundance of a bird species sensitive to a given disturbance was not compensated by the abundance of the remaining species (i.e. no density-compensation, Larsen et al. 2005), as occurs under field conditions in our study system (García and Martínez 2012). In addition, we were interested in testing whether non-random scenarios of bird losses generated higher biases of seed dispersal functions compared to random scenarios. We thus compared the changes on seed dispersal components generated by scenarios of bird losses at the landscape units (i.e. 110 40 × 40 m blocks). Given that we wanted to generate scenarios with density compensation as in the previous section, we maintained the same number of bird tracks in simulations comparing random and non-random scenarios.

In order to better visualize the patterns emerging from each scenario, we smoothed the results of the scenarios of bird losses over seed dispersal components. We used the locally weighted scatterplot smoothing regression ('Loess' regression, hereafter; Clarke et al. 2009). The Loess regression fits a low-degree polynomial with a subset of the data, constructing a function describing the predicted y-values. Along bird loss (x-axis) and seed dispersal components (y-axis), we fitted and visualized the simulated results to a Loess regression (smoothing parameter = 0.95, fitted by least squares) within the R environment (<www.r-project.org>).
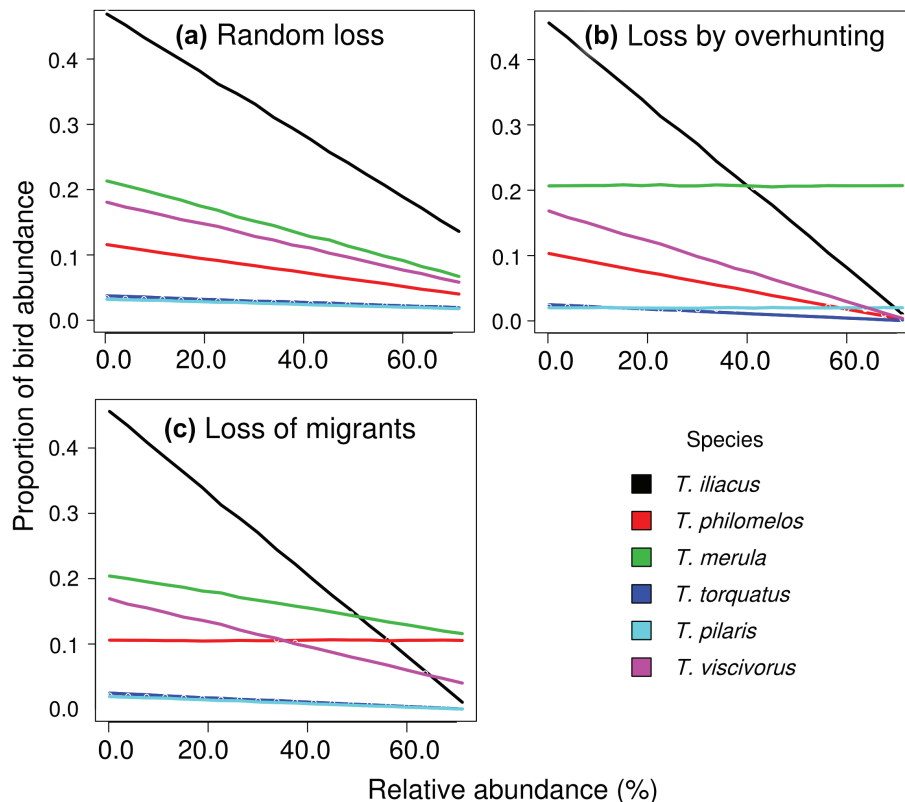

Figure 2. Relative abundance of species under different scenarios and percentages of bird loss (a) 'Random loss', (b) 'Loss by overhunting' and (c) 'Loss of migrant birds'. Coloured lines represent the abundance of each bird species averaged over 50 realisations. Starting from the initial bird composition observed in 2009, we modified the abundance of each species based on their sensitivities to each driver. For further details, see details for each scenario in Supplementary material Appendix 4.

Results

Effects of bird abundance and richness on seed dispersal

The observed frugivore assemblage generated positive linear relationships between bird density and seed density, and seed density in open microhabitats, whereas it showed a non-linear relationship for seed richness (see black dots in Fig. 3 upper panels). The assemblages of birds at increasing number of species with even abundances (coloured dots in upper panels) generated trends of seed dispersal in each landscape unit (i.e. 110 40 × 40 m blocks) similar to that of simulations of (uneven) observed bird abundances. Along an increasing gradient of bird richness, we found that the observed bird composition generated non-linear responses in seed density and richness, and linear trends in seed density in open microhabitats. The patterns generated by the observed

bird composition were similar to those of the simulations with four bird species evenly abundant (see Fig. 3 mid panels). However, detailed analyses showed that the values of all seed dispersal components generated by the observed bird composition tended to be higher than those predicted by the combination of four species evenly abundant (i.e. values are above the 1:1 reference line, and they thus generated negative component biases; see Fig. 3 lower panels).

The extinction of a bird species affected the values of seed dispersal at each landscape unit, but the magnitude of these changes differed among seed dispersal components. Compared with the observed bird compositions, poorer bird assemblages generated strong negative biases on seed density and seed richness, but weak negative or even positive biases on seed density in open areas (Fig. 4). The extinction of *Turdus philomelos* and *T. iliacus* generated the strongest biases on seed density and seed richness (Fig. 4), whereas that of *T. viscivorus* provoked the weakest bias in these two
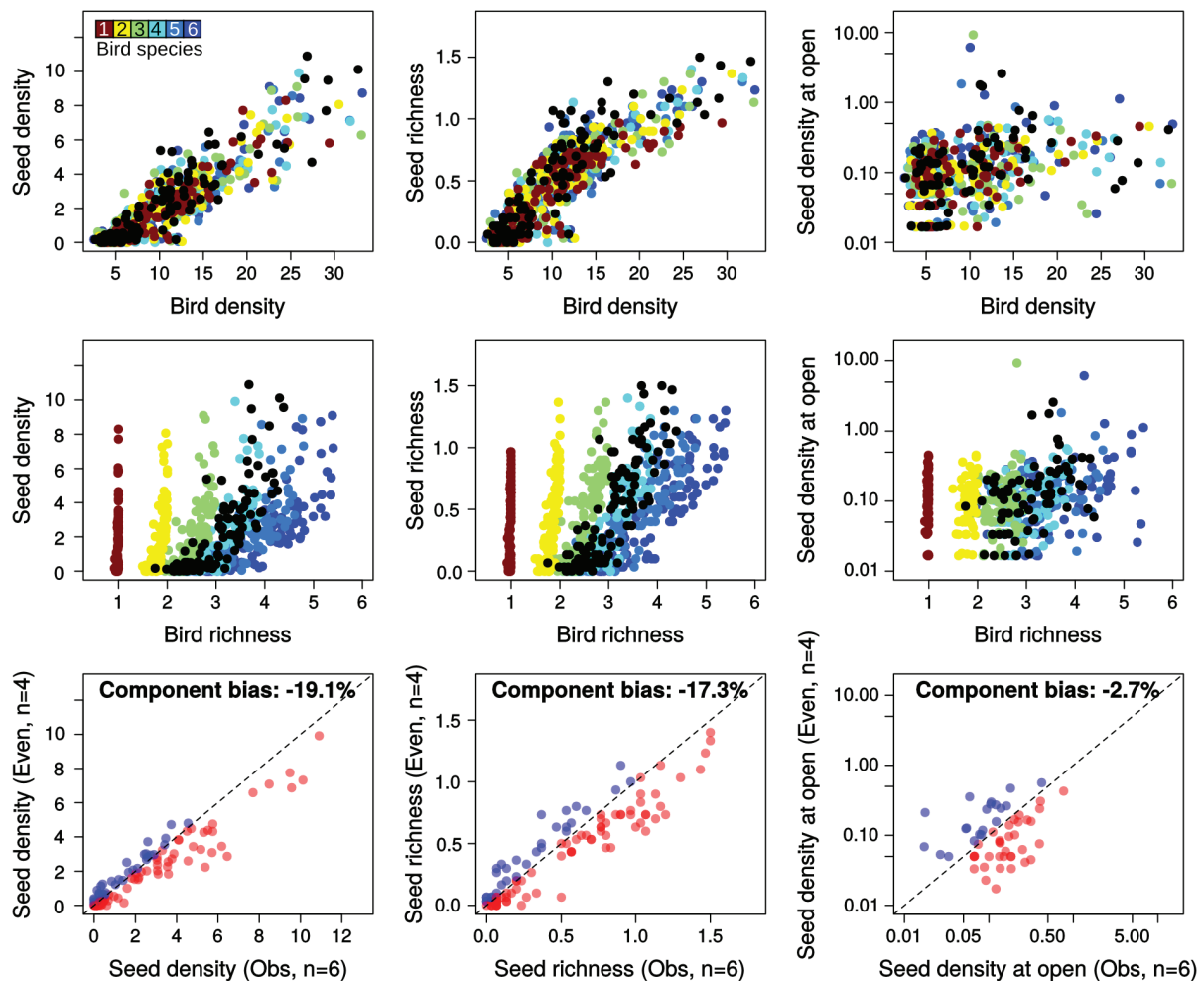

Figure 3. Effects of bird abundance and richness on seed dispersal. In upper and middle panels, black dots represent the result of simulations considering the effect of observed (uneven) bird composition to seed dispersal components calculated at each sampling landscape unit (i.e. 110 40 × 40 m blocks). Coloured dots represent simulations with randomly-assembled bird compositions at increasing species richness but always with even species abundance. In lower panels, we show the relationship between the two specific simulations previously performed above: the observed bird composition (x-axis) and the (even) four-species bird composition (y-axis) at each landscape unit. We computed the 'component bias' as the percentage of values above the 1:1 reference line between the two above-defined bird compositions. At each landscape unit, values above the reference line (dots in blue) mean that seed dispersal components performed better in bird composition of y-axis (i.e. component bias was positive), whereas values below reference line (dots in red) that dispersal components perform better in the bird composition of the x-axis (i.e. component bias was negative).
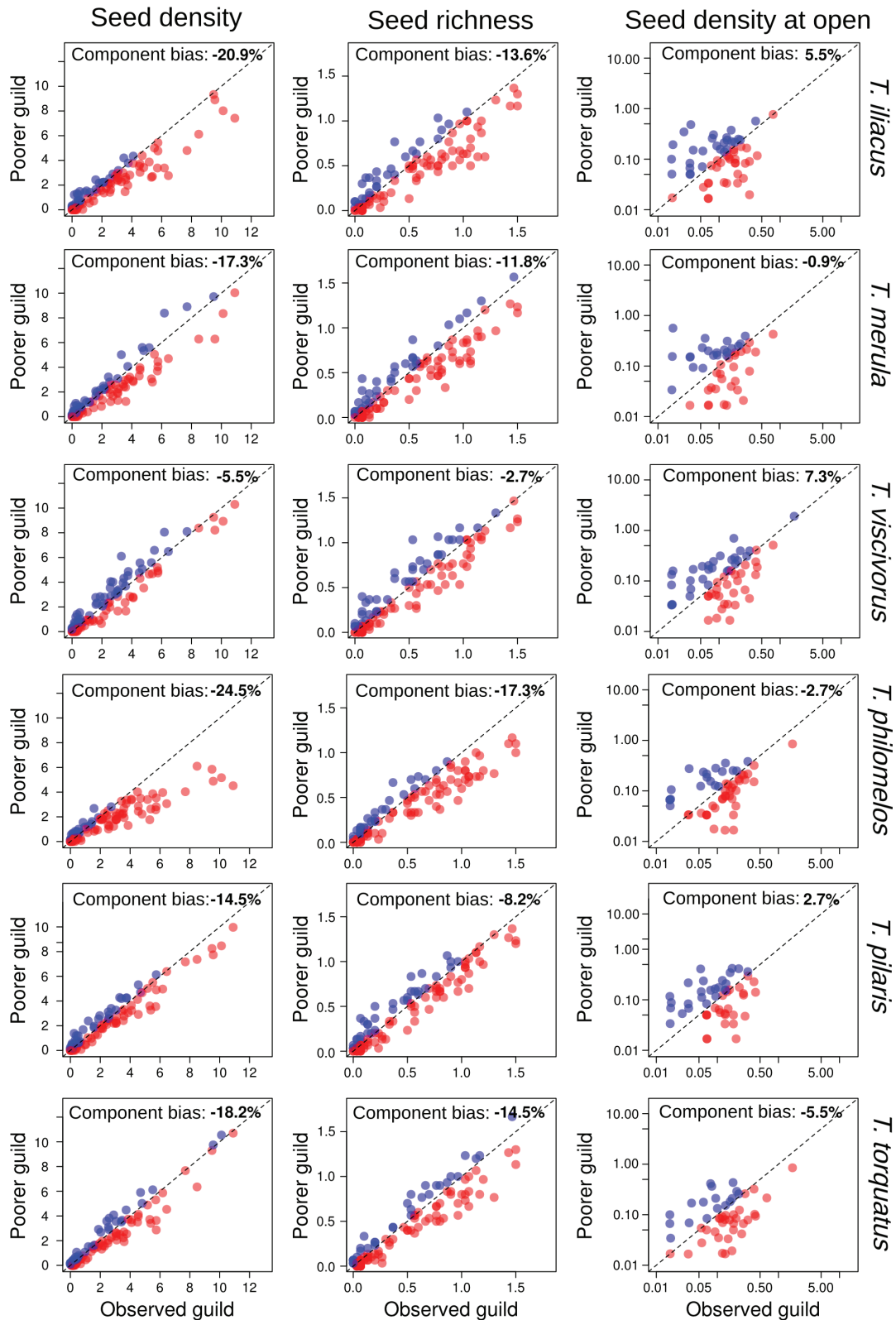
Figure 4. Effect of each bird species on seed dispersal on the extinction of bird species. For each landscape unit, we compared the relationship between the observed bird composition (x-axis) with poorer assemblages with the extinction of a single bird species (y-axis) at each landscape unit (i.e. 110 40 × 40 m blocks). For each row of panels, species extinctions were, *T. iliacus*, *T. merula*, *T. viscivorus*, *T. philomelos, T. pilaris* and *T. torquatus*. At each landscape unit, values of seed dispersal components with poorer bird assemblages (y-axis) performing better than observed bird composition (x-axis) were plotted in blue, whereas those worse were in red. For further conventions see Fig. 3.

seed dispersal components. Conversely, the strongest (positive) change in seed density in open microhabitats occurred when selectively removing *T. viscivorus* (Fig. 4).

Seed dispersal in scenarios of bird loss

Random and non-random scenarios (i.e. overhunting and fewer migrant individuals) of bird losses provoked reductions in all seed dispersal components averaged across the whole landscape. However, the response of seed dispersal showed different trends depending on the reduction of bird abundance (i.e. comparing random versus non-random bird losses), and the component of seed dispersal at the whole landscape (Fig. 5, upper panels). Seed density and seed density in open microhabitats decreased linearly along the gradient of bird losses, whereas seed richness decreased
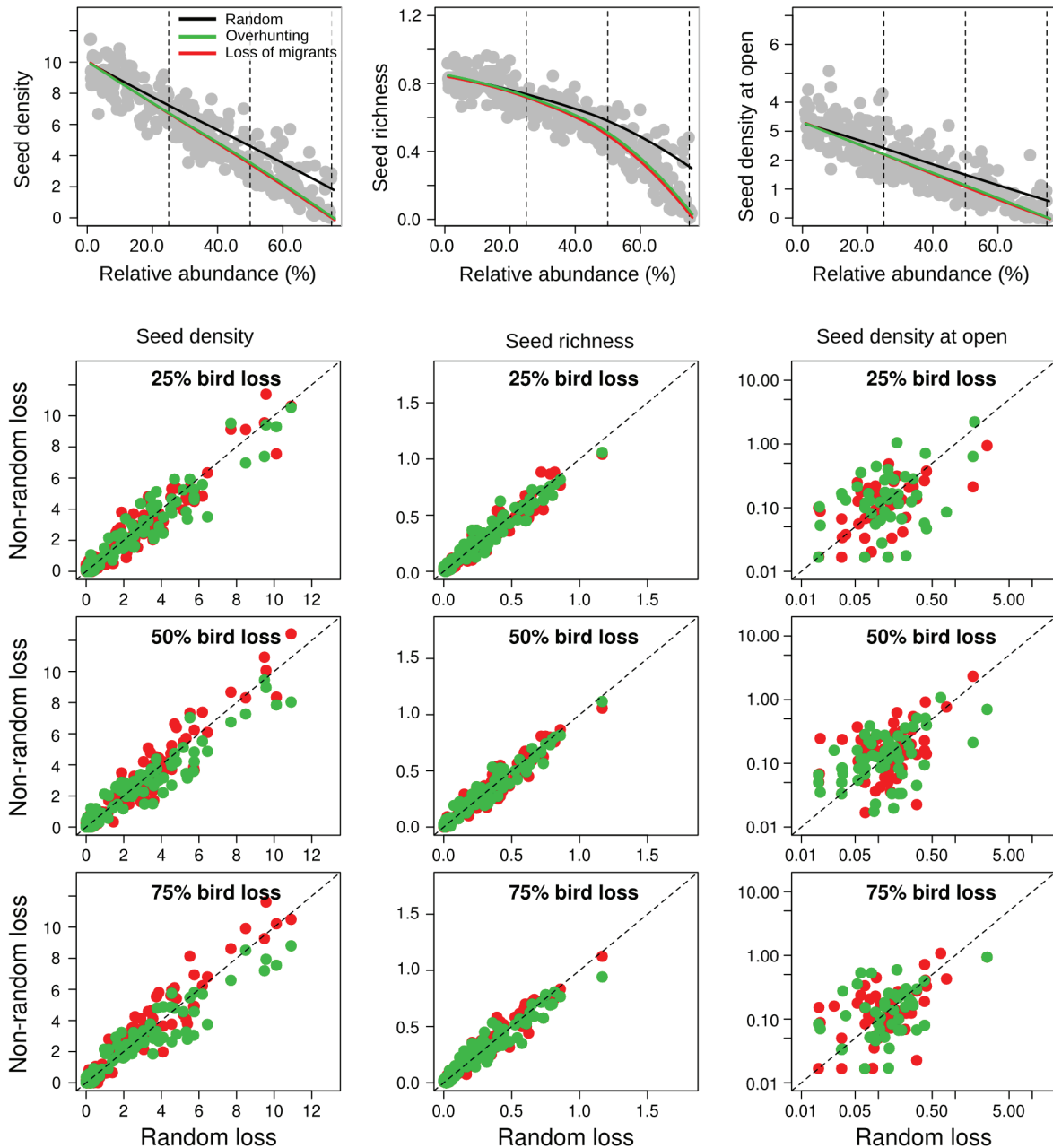

Figure 5. Changes on seed dispersal components by a random and two non-random scenarios of bird loss, namely 'Random loss', 'Loss of species by overhunting' and 'Loss of migrant species'. Simulations started with the observed bird composition, and we reduced bird species abundance for each scenario (see Fig. 2 for reduction of bird abundance for each species). In upper panels, grey dots represented the reduction of bird abundance of all scenarios averaged at the whole landscape; for the sake of clarity, we show a 30% random subset of all simulations. Coloured lines represent the results of each scenario fitted to a Loess regression (mean ± 95% CI interval). In the rest of panels we compared at each landscape unit (i.e. 110 40 × 40 m blocks) the relationship between the random (x-axis) with the two non-random scenarios (y-axis) for each interval of bird loss shown above (i.e. 0.25%, 0.50 and 0.75% of bird losses). At each landscape unit, values of seed dispersal components of non-random scenarios (y-axis) performing better than random scenarios (x-axis) were plotted in green, whereas those worse were in red. For further conventions see Fig. 3.

non-linearly, and sharply beyond 50% of bird loss. On average, non-random bird losses provoked stronger decays in seed dispersal than random losses (particularly in seed richness, due to the above-mentioned non-linear trend; Fig. 5 upper panels).

At each landscape unit we compared the values of the different seed dispersal components, between random and non-random scenarios of bird losses maintaining a constant number of total bird tracks. The values of seed density generated by non-random scenarios did not match those emerging from random losses, notably beyond the 50% of bird losses (Fig. 5). For instance, 'loss of migrant species' led to higher biases in seed densities than those generated by random losses, whereas 'loss by overhunting' led to lower biases on seed density than those provoked by random scenarios. Neither seed richness nor seed density in open microhabitats after non-random bird losses differed from random losses.

Discussion

We studied the variability in seed dispersal function of six frugivorous bird species, and the sensitivity of seed dispersal to frugivore losses. Using simulation models, we integrated the species variability in behaviour, habitat preferences, and sensitivity to alterations, with the aim of predicting changes in seed dispersal after bird losses. In our simulation experiments we varied species abundances and richness, allowing exploration of factors that are usually confounded in the majority of observational studies. We found that seed dispersal provided by an impoverished (four equally abundant species) frugivore assemblage was equivalent to that generated by the observed frugivore assemblage. Nevertheless, the loss of a single species was able to change some components of the seed dispersal function. Additionally, seed dispersal components varied according to intrinsic factors (i.e. related to the specific activity of birds and their sensitivity to disturbances), and they were also affected by extrinsic factors (i.e. extinction drivers of global-change) provoking selective bird losses.

Correlational or experimental studies on ecological processes across gradients of community composition are useful when formulating hypotheses on the link between biodiversity and ecosystem functions, and in the detection of changes in ecosystem properties due to anthropogenic disturbances creating new combinations of species traits (Wardle et al. 2011, Luck et al. 2012). Here, we found positive effects of the abundance and richness of frugivore species in seed dispersal properties, in line with previous observational studies in the same system (García and Martínez 2012). Our simulation experiments show that the observed bird composition (i.e. richer in species but with uneven abundances) provided higher values in seed density and richness than poorer, but with evenly abundant species, frugivore assemblages. Results also highlight the higher values of seed dispersal function provided by richer bird compositions and the complementarity of functional traits in the majority of species. Similarly, previous studies on this system have suggested that both quantitative and qualitative aspects of seed dispersal (sensu Schupp et al. 2010) depend on the variability in the activity and behaviour of frugivorous thrushes (Martínez et al. 2008, García et al. 2013, Morales et al. 2013). In temperate forests, as is our case, frugivore assemblages are relatively species-poor and we can expect a low redundancy in the seed dispersal function; this contrasts with tropical forest, which have high redundancy due to their high species richness (Loiselle et al. 2007).

By simulating the extinction of single bird species, we assessed the impact of each on seed dispersal. For instance, we found that the extinctions of *Turdus iliacus* and *T. philomelos* notably affected the density and richness of seeds arriving at each landscape unit, whereas extinctions of *T. viscivorus* affected the density of seeds in open microhabitats. These three species are abundant and have functional roles not shared by the rest of the frugivore assemblage (Fig. 4), and we suggest that extinction of rarer species would not produce such strong changes in seed dispersal. Our simulation model consisted of a small number of bird species (thrushes), and this may limit the generalization of the present results. Considering the whole community of frugivores (seven additional mammal species) and fleshy-fruited plants (five additional species) of our study system, it would certainly add new functional contributions to the present system (Peredo et al. 2013). Nevertheless, we expect that this would result in low discrepancies with the seed dispersal components calculated here as fruit dietary overlap between mammals and thrushes is very low, at least for our three fleshy-fruited trees (Peredo et al. 2013).

The specific cause of species extinction, and the order in which individuals are lost, can affect ecological dynamics in natural systems (Solan et al. 2004, Bunker et al. 2005, Larsen et al. 2005, Hillebrand and Matthiessen 2009). Here we predict that different reductions in the abundance of frugivorous birds will have differential effects on the seed dispersal function. Those functional losses were expressed as whole-landscape averaged values and ranged from linear (seed density and seed density in open microhabitats) to non-linear (seed richness). We were interested in calculating seed dispersal changes under potential real-world conditions, and we thus assumed no density compensation in our frugivore assemblage; under field conditions there is no evidence of competition for fruit resources among the species of thrushes, and there is no evidence of density compensation in the wild (as the abundances of the different species of thrushes have been found to correlate positively across space; García and Martínez 2012). In essence, our results mean that for some aspects of seed dispersal, the aggregated whole-landscape values of the function depend on the additive, non-redundant role of all bird species, whereas for other components, the functional roles of different species are redundant. In addition, non-random scenarios generated, on average, larger reductions in seed dispersal than random scenarios, suggesting that the imposed reduction on bird abundance by random losses affected less those frugivore species with proportionally stronger effect on the seed dispersal function, as occurs in other studies evaluating species extinctions and functional decays (Gross and Cardinale 2005). Stronger functional changes in community performance occur when species sensitivity to alterations are associated to their functional outcomes (Hillebrand and Matthiessen 2009). For instance, McIntyre et al. (2007)

perform simulation experiments to test the effect of fish extinction drivers on the recycling of nutrients and found that extinctions of species with a combination of high functionality and sensitivity to disturbances can rapidly diminish nutrient recycling.

When comparing random with non-random scenarios at the landscape unit, we predict that non-random bird losses will produced stronger effects on seed density, notably beyond 50% changes in bird species composition: this result is likely the consequence of the late loss of key species in functional terms as we found low functional decays (i.e. high resilience) with low bird losses. The latter simulation of bird losses compared landscape units and took into account density-compensation of frugivore abundance (Fig. 5 lower panels), with stronger losses of non-random scenarios along gradients of bird losses. Likewise, simulations of bird losses agreed at different scales of analysis (i.e. whole landscape and landscape units; Fig. 5), meaning that functional decays of seed dispersal are the consequence of a combination of species-based functional differences, and not just the consequence of numerical bird abundance. Specifically, we assumed that overhunting strongly affected all bird species (except *T. merula*), and we found that generated proportionally lower seed density in each landscape unit. Conversely, the loss of migrant birds primarily affected *T. iliacus*, and the remaining species of the frugivore assemblage provided a seed dispersal function biased towards higher seed density. In any case simulations at the landscape unit were performed with density-compensation of bird abundance, suggesting that the different sign of the bias of non-random scenarios may generate divergent functional outcomes, as the net effect in seed dispersal function is consistent and negative in both scenarios of bird losses (Fig. 5 upper panels).

Our results further highlight that it is imperative to relate species with singular functions to probable non-random disturbances (i.e. overhunting and reduced arrival of migrant birds), and how such species losses could entail synergistic impacts on natural communities. Additionally, mobile species are sensitive to landscape alterations (i.e. habitat loss and fragmentation), and these disturbances may act in combination with various drivers of global change (e.g. overhunting, climate change; as shown in the present work). Field data in the same study system showed that quantitative components of seed dispersal (i.e. seed density) had a sigmoidal relationship with bird richness, whereas qualitative components (i.e. seed arrival in open microhabitats) increased linearly with frugivore richness (García and Martínez 2012, Schleuning et al. 2015). This empirical pattern agrees with our simulation experiments at the scale of landscape units, supporting the idea that the species traits shape the seed dispersal patterns (i.e. behaviour, activity, physiology and spatial and temporal sensitivity of birds to disturbances) in combination with the landscape configuration of our study site (i.e. following a gradient of forest loss) are responsible for the patterns observed in the field. To this end, the analysis of simultaneous drivers of species decline could provide a greater breadth of conditions to test the effects of global change on ecological functions, and a more realistic approximation of future conditions (Tylianakis et al. 2008).

Concluding remarks

It is well established that we need to identify global change disturbances which have disproportionate impacts on biodiversity and ecosystem functions (Duffy 2003, Elmqvist et al. 2003, Naeem and Wright 2003). Even though we analysed a small trophic assemblage of frugivores, it is clear that frugivore decreasing abundances and extinctions provoke strong losses in the seed dispersal service (McConkey et al. 2011, Farwig and Berens 2012), that those functional losses were consistent (i.e. these seed dispersal components did not vary with different scenarios of bird loss) under different global-change scenarios, but different components of seed dispersal function (such as density and richness of dispersed seeds, and seed density out of the forest) were unevenly affected. Many ecosystem services such as pollination, pest control, and forest regeneration depend on animals (Şekercioğlu et al. 2004, Kremen et al. 2007, Karp et al. 2013), and are thus influenced by their behaviour, activity, physiology, and spatial and temporal sensitivity to disturbances. In consequence, the applicability of mechanistic frameworks to predict ecosystem services is certainly broad as this approach is able to go beyond species richness, and estimate functional diversity seen as the different contribution of each species to ecosystem functions. Future research using traits accounting for inter-specific variability in the activity and sensitivity to disturbances is thus needed to gain insights about the changes in ecosystem functions underlying the biodiversity loss resulting from responses to global change (Balvanera et al. 2006, Dobson et al. 2006, Díaz et al. 2013).

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