Long-term demographic consequences of a seed dispersal disruption

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The loss or decline of vertebrate frugivores can limit the regeneration of plants that depend on them. However, empirical evidence is showing that this is still very scarce, as functionally equivalent species may contribute to maintain the mutualistic interaction. Here, we investigated the long-term consequences of the extinction of frugivorous lizards on the population persistence of a Mediterranean relict shrub *Cneorum tricoccon* (Cneoraceae). We examined the demographic parameters among 26 insular and mainland populations, which encompass the entire plant distributional range, comparing populations with lizards with those in which these are extinct, but in which alien mammals currently act as seed dispersers. Plant recruitment was found to be higher on island populations with lizards than on those with mammals, and the long-term effects of the native disperser's loss were found in all vital phases of plant regeneration. The study thus gives evidence of the cascading effects of human-induced changes in ecosystems, showing how the disruption of native ecological processes can lead to species regression and, in the long term, even to local extinctions.

Keywords: biological invasions; *Cneorum tricoccon*; seed-disperser extinction; islands; mutualisms; saurochory

1. INTRODUCTION

The loss or decline of vertebrate frugivores occurring at a global scale can have important negative consequences for plants that depend totally or partially on them for their regeneration [1,2]. Seed dispersal disruptions are indeed increasingly being reported from different ecosystems, especially from islands [3,4]. However, few studies yet provide empirical evidence of the long-term costs of such disruptions. Specifically, seed dispersal disruptions may lead to the loss of genetic variability due to genetic drift, decreased fitness and reduced potential to adapt to changing environments; such genetic effects have yet been poorly investigated [5]. Likewise, the long-term demographic effects of the loss of vertebrate dispersal agents for the insular plants that depend upon them are very poorly known [6]. Changes in plant regeneration after a seed dispersal disruption may not become evident for a long time, especially for long-lived species, or may even go unnoticed, as functionally equivalent frugivorous species (either native or alien) may contribute to maintain the mutualistic interaction [7,8].

Among the different causes of mutualistic disruptions, the introduction of alien species is frequently reported [3,9,10]. In many islands of the world, there have been a great number of plant and animal introductions since the arrival of man to them, with detrimental consequences for the native biota. In particular, the introduction of vertebrates has had the most harmful impacts, leading to species extinctions (mainly animals) [11].

Well-known cases include the introduction of snakes in Guam island, which dramatically reduced bird numbers, some of which had an important role as pollinators and dispersers [12], and the introduction around 1870 of mammalian predators in the North Island of New Zealand [13], which also caused the extirpation of some bird species and in turn hampered ecosystem services such as pollination [14], and possibly seed dispersal as well [15].

A particular type of plant–animal interaction mainly described from islands [16] and threatened by invasive species [3] is seed dispersal by lizards (saurochory). Studies examining the tightness of plant–lizard mutualisms are rare [17], and thus, for most systems, we do not have the information needed to predict the implications of the disruption in such interactions.

In the Balearic Archipelago, inhabited by humans since around 2000 BC [18], the introduction of carnivores such as weasels (*Mustela nivalis*), pine martens (*Martes martes*), genets (*Genetta genetta*) and cats (*Felis catus*), possibly added to the effect of introduced snakes, led to the extinction of endemic lacertid lizards of the genus *Podarcis* in the two largest islands, Mallorca and Menorca, and also has reduced lizard densities in the other insular populations [19,20]. These lizards are important pollinators and seed dispersers of a variety of plants [21], and have established close relationships with some species, especially consuming their fruits and dispersing the seeds to suitable sites for germination and growth. In turn, some of the alien carnivores—such as pine martens and genets—eat fleshy fruits and act as seed dispersers, although their seed dispersal service is likely to differ from that provided by lizards, possibly affecting plant regeneration [22].
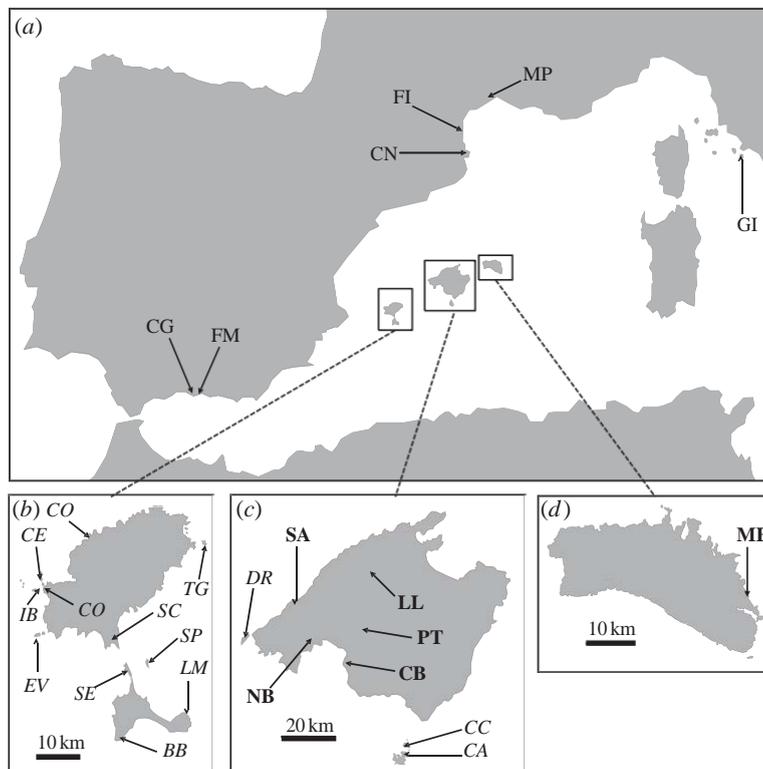
Figure 1. Map showing the distribution of Cneorum tricoccon populations examined in this study. (a) Abbreviations of populations with unknown dispersers are shown in normal type. (b–d) In the Balearic Islands, abbreviations of populations dispersed by lizards are shown in italics while those of populations dispersed by mammals are shown in bold type. Balearic Islands: (b) Eivissa and Formentera (north and south islands, respectively), (c) Mallorca and (d) Menorca. Full names and locations are given in the electronic supplementary material.

One of the plant species known to have a tight mutualism with lizards and currently dispersed also by alien mammals is C. tricoccon L. (Cneoraceae), a shrub distributed in the western Mediterranean Basin [23]. In this study, we evaluate the consequences of lizard extinction for plant population regeneration and assess to what extent alien mammals can replace their seed dispersal function. For this, we investigate the regeneration status of extant populations across the entire distributional range of the species. Specifically, we compare different demographic parameters across populations with lizards with those in which they are no longer present (but in which alien mammals act as seed dispersers), hypothesizing that plant regeneration will be higher in the former.

2. MATERIAL AND METHODS
(a) Study species
Cneorum tricoccon L. (Cneoraceae) is a perennial shrub, approximately 1 m tall, although some individuals can reach up to 2 m (see the electronic supplementary material, figure S1). The species represents a relict species of the flora that evolved during the early Tertiary under tropical conditions [24,25]. The fruit consists of three or (more rarely) four cocci (locules of a syncarpous ovary). Mature fruits, red coloured, are seen from about mid-March to mid-June, although the ripening peak is usually in April. Each coccus is functionally a drupe that measures, on average (+ s.d.), 5.7 + 0.054 mm (n ¼ 315) in cross diameter and weighs 0.139 + 0.003 g (n ¼ 315). Fruits that are not consumed can remain on the plant for long periods, often more than a year; they either dry up or are infested by a fungus that turns

them black. Although fruits of C. tricoccon are of the size and colour usually chosen by passerine birds, these animals do not consume them, probably owing to the high amount of secondary compounds (mainly tannins) in their pulp [22].

In the Balearic Islands, seed dispersal of C. tricoccon is mostly mediated by endemic lacertid lizards: Podarcis lilfordi and Podarcis pityusensis [22]. Podarcis siculus inhabits Giannutri island [26] and is presumably its main seed disperser there (A. Traveset & A. Valido 2004, personal observation). Introduced carnivorous mammals (such as Martes martes or Genetta genetta) are currently the main dispersers in the Balearic islands where lizards are extinct [22].

In continental Spain, scats of stone martens (Martes foina) have been found containing intact seeds of C. tricoccon (J. Calvo 2003, unpublished data), suggesting that this carnivore acts as a legitimate disperser of this species. The ocellated lizard Timon lepidus (Lacertidae) also consumes the fruits of C. tricoccon in some localities in southern Spain (J. A. Hódar 2002, personal communication) and we found a scat of an unidentified carnivore mammal with C. tricoccon seeds in it. Finally, C. tricoccon seeds have been occasionally observed outside ant nests, which suggests that these insects probably act as secondary dispersers [22] (J. Calvo 2003, unpublished data), and have also been occasionally found in gulls' regurgitates [27]. No data exist on seed dispersal of this plant in the other continental areas in which it is found (France and Italy).

(b) Study populations
We gathered data of C. tricoccon plants from 26 populations spanning the distribution range of the species (figure 1); 20 were located in 14 islands in the Balearics, where the species

is most common, five in relict mainland localities (three in the Iberian Peninsula and two in France) and one in Giannutri Island (Tuscan Archipelago in Italy). Table S1 in the electronic supplementary material shows the list of all localities studied with their geographical coordinates, and the main climatic variables in each one. In all these sites, C. tricoccon usually inhabits coastal maquis or shrublands, dominated by species such as Pistacia lentiscus, Olea europea, Rhamnus alaternus, Cistus monspeliensis and Rosmarinus officinalis, usually in calcareous soils. In the Balearic Islands, the species has also colonized the interior of the larger islands, and it is often found in the understorey of oak forests (Quercus ilex L.) up to an altitude of around 1000 m a.s.l. [22]. See the electronic supplementary material for further details on the distribution of C. tricoccon in the Mediterranean Basin.

(c) Demographic parameters

We gathered biometric data on all individuals in small populations (minimum $n = 16$ individuals) and a maximum of 152 (haphazardly chosen) in large populations (hundreds of individuals). From each individual plant ($n = 2544$), we recorded the maximum height (h), and the longest (D) and perpendicular (d) canopy diameter, estimating from these its canopy volume as $2/3 \times p \times (h \times D/2 \times d/2)$. We also measured the trunk diameter of individuals, although in some cases this was not possible (in recently emerged seedlings or in individuals in which branching started below the ground). Height and canopy diameter measurements were made to the nearest cm, whereas trunk diameter was measured to the nearest 0.01 mm (using a digital calliper). Additional information such as the reproductive status and the fruit crop was also noted. For seedlings, we further recorded the microhabitat in which it was found (in open interspaces, under the parent plant, under shrubs or under trees). Sampling was carried out at the peak of the fruiting period of the plant (June–July) in all populations.

In order to characterize the regeneration dynamics at the population level, we used three demographic parameters: the ratios of seedlings to adults, saplings to adults and juveniles to adults. They can be considered as relative measures of population natural regeneration: the larger the values, the higher the recruitment population rates. We considered as seedlings recently emerged individuals (i.e. less than 1 year old; mean height = 3 cm) as well as those with a trunk diameter less than 3 mm (mean height = 15 cm and mean diameter = 12 cm), which were probably 1–3 years old. The rest of individuals were considered as established (saplings, juveniles and adults; $n = 1933$), as the seedling stage is the most critical stage for recruitment of woody species in the Mediterranean ecosystem [28]. The categorization of each individual was made based on its trunk diameter, as the canopy volume is more susceptible to being shaped by environmental conditions (e.g. shade) and plant history (e.g. resprouted plants after serious disturbances). We were able to measure the trunk diameter in 92.8 per cent of established individuals ($n = 1933$; see electronic supplementary material, figure S2); from the rest of the individuals ($n = 140$), this variable was estimated by using linear regressions between $\log_{10}$ canopy volume (obtained for all individuals) and $\log_{10}$ trunk diameter, because both variables were highly correlated (all populations pooled: $r^2 = 0.68$, $p < 0.001$, $n = 1793$). We additionally performed separate regressions for each population as both the slope and the

intercept may depend on local environmental factors; they were performed with 16–93 individuals per population and a high correlation was also observed in all of them (mean $r^2 = 0.72$, range $= 0.54$–0.91; all p-values < 0.001).

Saplings were considered as such when the trunk diameter was less than 6.3 mm ($\log_{10}$ trunk diameter less than 0.8); 36 per cent of individuals classified as saplings bore a few fruits (median $= 3$). Juveniles had trunk diameter between 6.3 and 16.0 mm ($\log_{10}$ trunk diameter: 0.8–1.2); 59 per cent of them bore a few fruits (median $= 8$). Finally, plants were considered as adults when their trunk diameter was greater than 16.0 mm ($\log_{10}$ trunk diameter greater than 1.2); 87 per cent of these plants bore fruit, with crops ranging from several dozen to a few hundred fruits (median $= 45$).

(d) Climatic data

In order to know the effect of differential climatic conditions among populations that might account for differences in regeneration (and irrespective of the presence of the type of seed disperser), we obtained, for each population, the mean maximum temperature of the hottest month (t_{max}), mean minimum temperature of the coldest month (t_{min}) and annual precipitation (pp) from the nearest (less than 20 km) meteorological stations with enough data (range $= 15$–30 years). We then calculated Emberger's [29] index of aridity (Q) as $Q = (2000 \times pp)/(t_{max}^2 - t_{min}^2)$. Values of Emberger's index were logarithmically transformed for statistical analyses because Q increases nonlinearly in more mesic habitats [30]. The resulting variable refers to $-\ln Q$, being positively correlated with actual aridity and negatively correlated with primary productivity in arid and semi-arid areas [29].

(e) Statistical analyses

We performed two sets of analyses. The first included all sampled populations, and tested for differences in the three demographic parameters between islands and the mainland. The second set included only populations for which seed dispersers are well known (i.e. Balearic Islands; $n = 20$), and tested for differences between lizard-dispersed populations and mammal-dispersed ones. In both sets of analyses, we used generalized linear models (GLMs), with the population type (i.e. 'island versus mainland' and 'lizard versus mammal') as the main fixed factor and the population identity nested within the type. A binomial distribution and logit link functions were used with seedlings, saplings or juveniles coded as '1', and adults as '0'. Analyses were performed with STATISTICA v. 6.

3. RESULTS

All demographic parameters analysed were highly variable among populations (all p-values < 0.001) for both sets of models (either including all populations or only Balearic ones; table 1; see also figure 2 and electronic supplementary material, figure S3(ii)). Island populations showed a significant approximately 2.2-fold higher seedlings : adults ratio than mainland populations (table 1 and figure 2), although no significant differences existed in the other demographic parameters (p-values < 0.14). Remarkably, in the Balearics, the ratios were significantly higher in lizard-dispersed than in mammal-dispersed populations (table 1 and figure 2), reflecting a lower recruitment and an older age structure in the latter. This was also supported by the finding of wider adult trunk diameters in
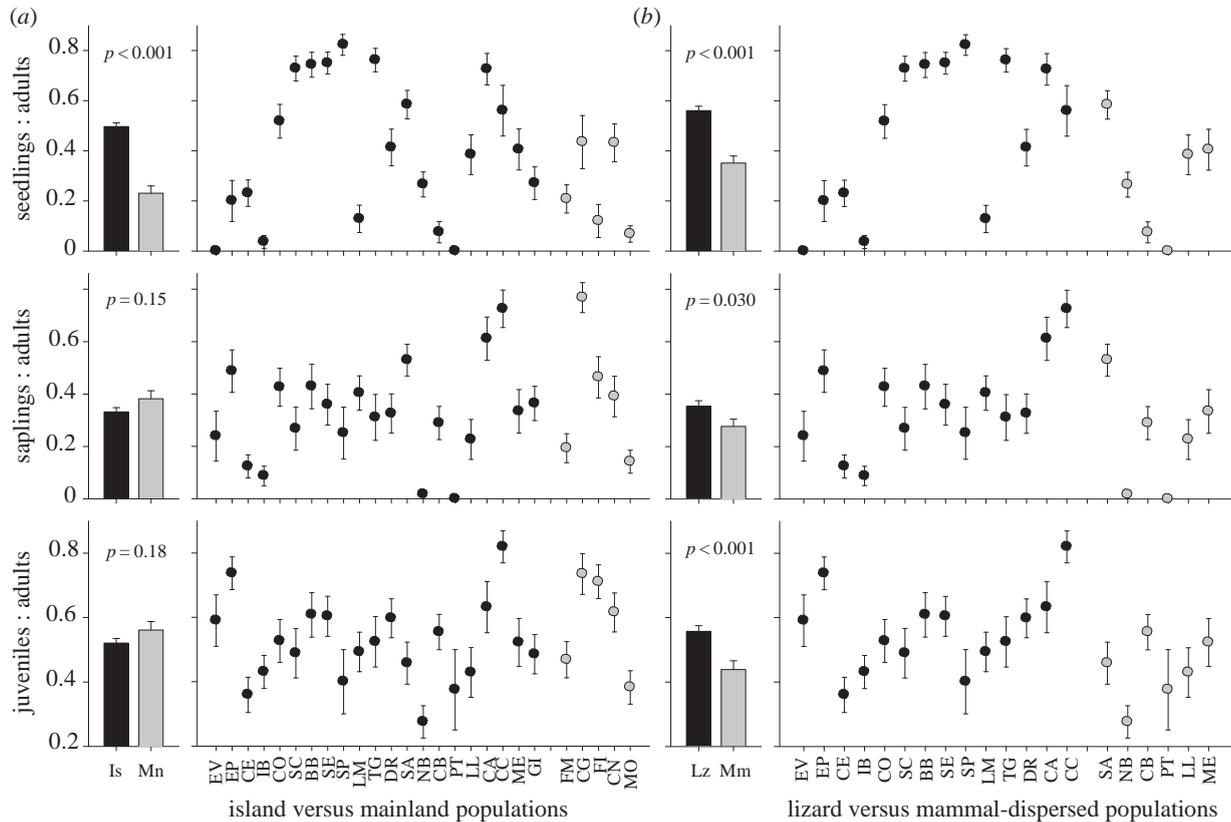
Figure 2. Variation in the demographic parameters examined (a) between island and mainland populations (black and grey columns, respectively) and (b) between lizard- and mammal-dispersed populations (black and grey columns, respectively), as well as among populations within each category. p-values from GLMs analysing differences between population types are shown. Within each category, populations are arranged from west to east. Sites codes match those in figure 1.

Table 1. Results of nested GLMs analysing differences in demographic parameters among Cneorum tricoccon populations for the two sets of data: (a) including all populations, differences between island (Is) and mainland (Mn) populations, and among populations within each category; (b) including only data from the Balearic Islands, differences between lizard- (Lz) and mammal-dispersed (Mm) populations, and among populations within each category. p-values ₌ 0.05 are shown in bold type. Ratios were modelled with binomial distribution and logit link function; seedlings, saplings or juveniles ¼ 1, adults ¼ 0.

| | (a) all populations | | | | (b) Balearic populations | | | |
| | Is versus Mn | | among populations | | Lz versus Mm | | among populations | |
demographic variable (ratios)	x_1^2	p	x_{24-25}^2	p	x_1^2	p	x_{18-19}^2	p
seedlings : adults	52.2	<0.001	382.2	<0.001	37.4	<0.001	309.5	<0.001
saplings : adults	2.2	0.142	204.6	<0.001	4.7	0.030	134.9	<0.001
juveniles : adults	1.8	0.177	112.4	<0.001	12.9	<0.001	69.1	<0.001

mammal-dispersed populations (mean + s.e.: 27.1 + 1.0 mm) compared with lizard-dispersed ones (23.7 + 1.0 mm; x_1^2 ¼ 17:1, p ₌ 0.001).

The demographic parameters studied were neither significantly associated with the mean annual precipitation (pp) nor with aridity (−lnQ), either pooling all populations in the correlation analysis or using only data from the Balearics (Spearman's r_s: all p-values ₌ 0.15, n ¼ 5–26).

Finally, we found a larger fraction of seedlings distributed across different microhabitats, including open interspaces and below other shrub species, in lizard-dispersed populations than in mammal-dispersed populations (table 2); in the latter, the largest fraction of seedlings was found in open spaces under pine trees.

4. DISCUSSION

Our results show that the regeneration of C. tricoccon is much higher on islands in the presence of lizards as compared with islands where alien carnivorous mammals are the only dispersers. Thus, lizards appear to be important mutualistic agents for this plant, and their loss appears to have affected seedling, sapling and juvenile establishment. Moreover, island populations show higher plant regeneration than the mainland ones; the lack of feasible information on mainland frugivores, however, leaves open the question of how important seed dispersal limitation is relative to other factors behind such island–mainland differences. The saplings : adults and juveniles : adults ratios are similar between islands and the mainland, indicating that seedling recruitment on the latter

Table 2. Distribution of seedlings across microhabitat (% of all seedlings) in populations that are dispersed by either lizards or mammals in the Balearic Islands (all populations pooled).

population type	Cneorum	open	shrub	tree
lizard-dispersed (n ¼ 285)	26.3	25.6	35.8	12.3
mammal-dispersed (n ¼ 93)	2.2	18.3	3.2	76.3

actually occurs, although it is possibly a rather stochastic event. A low recruitment, with seedlings being restricted to the canopy of parent plants, has been previously reported from three populations of C. tricoccon in the southeastern Iberian Peninsula [31], and in some populations, like Cap Norfeu (northeastern Spain), we recorded up to 70 per cent of seedlings beneath adults. Seedling herbivory has never been observed, which is attributed to the high level of secondary compounds in the leaves of this species [22].

Lizards are known to act as effective dispersers of other plant species, in the Balearics and elsewhere, moving seeds to sites where seedlings may have a greater probability of becoming adults, and thus playing a fundamental role in their regeneration [7,32,33]. Our results with C. tricoccon actually showed that seedlings were more distributed across different microhabitats in lizard-dispersed populations than in mammal-dispersed populations. In the latter, pine martens are mainly responsible for the dispersal, while genets defecate mostly in latrines within caves [7,22]. In a previous study, we found that pine martens remove a much lower proportion of C. tricoccon fruits from the plants than lizards [23], and thus, in quantitative terms, they are less effective than lizards; however, their qualitative importance as seed dispersers remains unknown. What is known is that these alien mammals are moving seeds to habitats (pine woodlands) where Podarcis lizards are rarely present as they are mostly restricted to shrubland habitats. Therefore, even though alien dispersers might replace native ones to some extent, as found in other systems [34], the seed dispersal patterns of C. tricoccon appear to have changed with these novel interactions.

Our study further suggests that the Balearic Islands might act as a refuge for this Tertiary relict because of the prevalent plant–lizard mutualistic interaction. The fossil seeds of C. tricoccon found in palaeontological deposits from the Pliocene [35] in the sites of Menorca (with extinct lizards) where the plant is no longer present offers clear evidence of the more widespread distribution that this species had in the past. We attribute the shrinking of C. tricoccon in Menorca to the disappearance of P. lilfordi, as it seems to have happened with at least one other plant species, the endemic and threatened shrub Daphne rodriguezii [6,7].

Given that saurochory is a common phenomenon on islands, it is likely that our results can be extended to other archipelagos where frugivorous lizards (or other reptiles) have been extinct or are currently threatened [17]. The high vulnerability of island biotas is usually associated with their small size and isolation, higher rates of human-driven habitat loss, and higher sensitivity to biological invasions and climate change [36]. Evidence is growing that focusing only on species conservation is not enough, and that in order to preserve and restore biodiversity, we need to maintain and re-establish the integrity of interactions (such as saurochory) between species [37]. More work is needed across different species and ecosystems to better understand the overall cost of mutualistic disruptions, but the evidence so far indicates that this is quite high.

REFERENCES

1 Babweteera, F. & Brown, N. 2009 Can remnant frugivore species effectively disperse tree seeds in secondary tropical rain forests? Biodivers. Conserv. 18, 1611–1627. (doi:10.1007/s10531-008-9546-6)

2 Wotton, D. M. & Kelly, D. 2011 Frugivore loss limits recruitment of large-seeded trees. Proc. R. Soc. B 278, 3345–3354. (doi:10.1098/rspb.2011.0185)

3 Traveset, A. & Richardson, D. M. 2006 Biological invasions as disruptors of plant reproductive mutualisms. Trends Ecol. Evol. 21, 208–216. (doi:10.1016/j.tree.2006.01.006)

4 Hansen, D. M. & Galetti, M. 2009 The forgotten megafauna. Science 324, 42–43. (doi:10.1126/science.1172393)

5 Calviñ o-Cancela, M., Escudero, M., Rodríguez-Pérez, J., Cano, E., Vargas, P., Velo-Antó n, G. & Traveset, A. In press. The role of seed dispersal, pollination and historical effects on genetic patterns of an insular plant that has lost its only seed disperser. J. Biogeogr. (doi:10.1111/j.1365-2699.2012.02732.x)

6 Rodríguez-Pérez, J. & Traveset, A. In press. Demographic consequences for a threatened plant after the loss of its only disperser. Habitat suitability buffers limited seed dispersal. Oikos. (doi:10.1111/j.1600-0706.2011.19946.x)

7 Traveset, A. & Riera, N. 2005 Disruption of a plant–lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. Conserv. Biol. 19, 421–431. (doi:10.1111/j.1523-1739.2005.00019.x)

8 McConkey, K. R. & Drake, D. R. 2006 Flying foxes cease to function as seed dispersers long before they become rare. Ecology 87, 271–276. (doi:10.1890/05-0386)

9 Kelly, D., Robertson, A. W., Ladley, J. J., Anderson, S. H. & McKenzie, R. J. 2006 The relative (un)importance of introduced animals as pollinators and dispersers of native plants. In Biological invasions in New Zealand (eds R. B. Allen & W. G. Lee), pp. 227–245. Berlin, Germany: Springer.

10 Davis, N. E., Dennis, J., O'Dowd, D. J., MacNally, R. & Green, P. T. 2009 Invasive ants disrupt frugivory by endemic island birds. Biol. Lett. 6, 85–88. (doi:10.1098/rsbl.2009.0655)

11 Sax, D. F. & Gaines, S. D. 2008 Species invasions and extinction: the future of native biodiversity on islands. Proc. Natl Acad. Sci. USA 105, 11 490–11 497. (doi:10.1073/pnas.0802290105)

12 Mortensen, H. S., Dupont, Y. L. & Olesen, J. M. 2008 A snake in paradise: disturbance of plant reproduction following extirpation of bird flower-visitors on Guam.

Biol. Conserv. 141, 2146 –2154. (doi:10.1016/j.biocon.
2008.06.014)

13 Innes, J., Kelly, D., Overton, J. M. & Gillies, C. 2010 Predation and other factors currently limiting New Zealand forest birds. N.Z. J. Ecol. 34, 86 –114.

14 Anderson, S. H., Kelly, D., Ladly, J. J., Molloy, S. & Terry, J. 2011 Cascading effects of bird functional extinction reduce pollination and plant density. Science 31, 1068 –1071. (doi:10.1126/science.1199092)

15 Kelly, D., Ladley, J. J., Wotton, D. M., Robertson, A. W., Anderson, S. H. & Wiser, S. K. 2010 Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit dispersal in New Zealand. N. Z. J. Ecol. 34, 66 –85.

16 Olesen, J. M. & Valido, A. 2003 Lizards as pollinators and seed dispersers: an island phenomenon. Trends Ecol. Evol. 18, 177 –181. (doi:10.1016/S0169-5347(03) 00004-1)

17 Valido, A. & Olesen, J. M. 2007 Importance of lizards as frugivores and seed dispersers. In Seed dispersal: theory and its application in a changing world (eds A. Dennis, R. Green, E. Schupp & D. Westcott), pp. 124 – 147. Wallingford, UK: CABI.

18 Alcover, J. A. 2008 The first mallorcans: prehistoric colonization in the western Mediterranean. J. World Prehist. 21, 19 –84. (doi:10.1007/s10963-008-9010-2)

19 Reumer, J. W. F. & Sanders, E. A. C. 1984 Changes in the vertebrate fauna of Menorca in prehistoric and classical times. Z Säugetierkunde 49, 321 –325.

20 Pérez-Mellado, V. et al. 2008 Population density in Podarcis lilfordi (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). Amph. Rept. 29, 49 –60. (doi:10.1163/15685380878 3431587)

21 Sáez, E. & Traveset, A. 1993 Fruit and nectar feeding by Podarcis lilfordi (Lacertidae) on Cabrera Island (Balearic Archipelago). Herp. Rev. 26, 121 –123.

22 Traveset, A. 1995 Seed dispersal of Cneorum tricoccon by lizards and mammals in the Balearic Archipelago. Acta Oecol. 16, 171 –178.

23 Riera, N., Traveset, A. & García, O. 2002 Breakage of mutualisms by alien species: the case of Cneorum tricoccon L. in the Balearic Islands (western Mediterranean Sea). J. Biogeogr. 29, 713 –719. (doi:10.1046/j.1365-2699. 2002.00719.x)

24 Maguinness, O. D. 1936 Relict species of Bas-Languedoc. J. Ecol. 24, 361 –371. (doi:10.2307/2256431)

25 Raven, P. H. 1973 The evolution of Mediterranean floras. In Mediterranean type ecosystems: origin and structure (eds F. Castri & H. A. Mooney), pp. 213 –224. Berlin, Germany: Springer.

26 Corti, C., Noistri, A., Poggesi, M. & Vammi, S. 1991 Biogeographical analysis of the Tuscan herpetofauna (Central Italy). Rev. Esp. Herp. 5, 51 –75.

27 Calviño-Cancela, M. 2011 Gulls (Laridae) as frugivores and seed dispersers. Plant Ecol. 212, 1375 –1383. (doi:10.1007/s11258-011-9913-3)

28 Gómez-Aparicio, L. 2008 Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings, and saplings in heterogeneous landscapes at different scales. J. Ecol. 96, 1128 –1140. (doi:10.1111/j. 1365-2745.2008.01431.x)

29 Emberger, L. 1955 Une classification biogéographique des climats. Trav. Inst. Bot. Montpellier 7, 3 –43.

30 Tieleman, B. I., Williams, J. B. & Bloomer, P. 2003 Adaptation of metabolism and evaporative water loss along an aridity gradient. Proc. R. Soc. Lond. B 270, 207 –214. (doi:10.1098/rspb.2002.2205)

31 Blanca, G., Cabezudo, B., Hernández-Bermejo, J. E., Herrera, C.M., Molero, J., Muñoz, J. & Valdés, B. 1999 Libro rojo de la flora silvestre amenazada de Andalucía. Tomo 1: especies en peligro de extinción. Consejería de Medio Ambiente. Sevilla, Spain: Junta de Andalucía.

32 Rodríguez-Pérez, J. & Traveset, A. 2010 Seed dispersal effectiveness in a plant –lizard interaction and its consequences for plant regeneration after disperser loss. Plant Ecol. 207, 269 –280. (doi:10.1007/s11258-009-9671-7)

33 Wotton, D. M. 2002 Effectiveness of the common gecko (Hoplodactylus maculates) as a seed disperser on Mana Island, New Zealand. N. Z. J. Bot. 40, 639 –647. (doi:10.1080/0028825X.2002.9512820)

34 Foster, J. T. & Robinson, S. K. 2007 Introduced birds and the fate of Hawaiian rainforests. Conserv. Biol. 21, 1248 –1257. (doi:10.1111/j.1523-1739.2007.00781.x)

35 Traveset, A., Quintana, J. & Alcover, J. A. 2005 Fossil seeds from the Pliocene of Menorca and Eivissa (Balearic Islands, western Mediterranean). Endins 27, 205 –209.

36 Kueffer, C., Daehler, C. C., Torres-Santana, C. W., Lavergne, C., Meyer, J.-Y., Otto, R. & Silva, L. 2010 A global comparison of plant invasions on oceanic islands. Perspect. Plant Ecol. Evol. Syst. 12, 145 –161. (doi:10. 1016/j.ppees.2009.06.002)

37 Kaiser-Bunbury, C. N., Traveset, A. & Hansen, D. M. 2010 Conservation and restoration of plant –animal mutualisms on oceanic islands. Perspect. Plant Ecol. Evol. Syst. 12, 131 –143. (doi:10.1016/j.ppees.2009.10.002)