



Research

Cite this article: Viana DS, Gangoso L, Bouten W, Figuerola J. 2016 Overseas seed dispersal by migratory birds. *Proc. R. Soc. B* **283**: 20152406.
<http://dx.doi.org/10.1098/rspb.2015.2406>

Received: 7 October 2015

Accepted: 20 November 2015

Subject Areas:

ecology

Keywords:

long-distance dispersal, seed dispersal, endozoochory, migratory birds, biogeography

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.2406> or via <http://rspb.royalsocietypublishing.org>.

Overseas seed dispersal by migratory birds

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Long-distance dispersal (LDD) promotes the colonization of isolated and remote habitats, and thus it has been proposed as a mechanism for explaining the distributions of many species. Birds are key LDD vectors for many sessile organisms such as plants, yet LDD beyond local and regional scales has never been directly observed nor quantified. By sampling birds caught while in migratory flight by GPS-tracked wild falcons, we show that migratory birds transport seeds over hundreds of kilometres and mediate dispersal from mainland to oceanic islands. Up to 1.2% of birds that reached a small island of the Canary Archipelago (Alegranza) during their migration from Europe to Sub-Saharan Africa carried seeds in their guts. The billions of birds making seasonal migrations each year may then transport millions of seeds. None of the plant species transported by the birds occurs in Alegranza and most do not occur on nearby Canary Islands, providing a direct example of the importance of environmental filters in hampering successful colonization by immigrant species. The constant propagule pressure generated by these LDD events might, nevertheless, explain the colonization of some islands. Hence, migratory birds can mediate rapid range expansion or shifts of many plant taxa and determine their distribution.

1. Introduction

Many species occupy vast areas of the Earth and show either continuous or disjunct distributions, suggesting that they are able to disperse over long distances, cross biogeographic barriers and colonize distant regions. Long-distance dispersal (LDD) is increasingly recognized as a potentially important mechanism shaping the distribution of biodiversity [1–4]. Although it is assumed to occur at relatively low frequencies, depending on the dispersal distance, LDD can operate from landscape to global scales and have important ecological and biogeographic consequences [5–7]. At the landscape scale, LDD promotes habitat connectivity, particularly in fragmented habitats, and thus regulates metapopulation and meta-community dynamics [8]. At broader spatial scales, from regional up to global scales, LDD might lead to range expansion or shifts (including biological invasions), and thus influence biogeographic and evolutionary processes [2].

For many sessile organisms that cannot actively move, most notably plants as well as many invertebrates and microorganisms, dispersal relies on the transport of propagules, such as seeds, resting eggs or spores, by different dispersal vectors, such as water, wind and animals. Propagules are usually dispersed at local scales; for example, seed dispersal distances typically range from 10 to 1500 m [9]. However, LDD operates over distances that potentially reach hundreds or thousands of kilometres [10]. In fact, passive LDD has been suggested to underlie several biogeographic patterns, including island (re)colonization [11,12] and the formation of disjunct distributions [13]. For instance, (i) sea-drifting seeds (pushed by ocean currents) of a pan-tropical plant (*Hibiscus pernambarucensis*) have been proposed to be responsible for the relatively low genetic differentiation between Atlantic and Pacific populations [14];

(ii) anisotropic wind patterns have been suggested to explain floristic assemblages in islands of the Southern Hemisphere [15]; and (iii) LDD events mediated by birds have been hypothesized to explain bipolar distributions, which is an extreme disjunct distribution pattern [13], and transoceanic distributions [16].

Since Darwin [17], migratory birds have been suggested to be involved in the LDD of a variety of organisms, mainly in aquatic ecosystems, where both epi- and endo-zoochory are frequent [18,19]. Other long-distance fliers, such as seabirds, have also been proposed as vectors of LDD between oceanic islands [11]. However, at present, there is only indirect evidence of the potential of migratory birds as LDD vectors, which is derived from phylo- and biogeographic patterns and anecdotal observations of seeds in the gut or plumage of migratory birds before or after active migration [11,20,21]. Quantitative evidence that migratory birds can actually disperse propagules during a migratory flight has been elusive, mainly due to the inherent difficulty of tracking birds and propagules that are engaged in migratory flight. We searched, collected and quantified seeds from hunted migratory birds to investigate whether overseas migratory movements of birds can mediate seed LDD. For this purpose, we used the 'sampling services' provided by the hunting activity of a wild population of Eleonora's falcons (*Falco eleonorae*) and last-generation tracking technology. These falcons prey on migrating birds flying over the ocean during autumn migration and store them in larders close to their nests. By analysing falcon movements and identifying seeds, we could safely conclude that seeds were carried from overseas locations and not ingested locally. Collected seeds were identified to the lowest possible taxonomic level according to DNA barcoding and morphological characteristics (see electronic supplementary material, table S1).

2. Material and methods

(a) Study system

The frequency of LDD was quantified by sampling the seeds found in the guts of birds actively hunted by Eleonora's falcons while migrating over the ocean. Eleonora's falcons breed on small Mediterranean islands located along major migratory flyways between Europe and Africa, on the Moroccan Atlantic coast, and on small islands in the eastern most Canary Islands [22]. Their breeding season spans from late July until mid-October and largely overlaps with the major period of autumn migratory flux of birds travelling to Africa. Eleonora's falcons prey almost exclusively on these migrating birds to raise offspring [22]. We carried out our work on the small island of Alegranza, which is the northern-most island of the eastern Canary Archipelago, and on two nearby, smaller islands (figure 1a). The Canary Islands are not located along a major migratory route; however, birds reach the Archipelago during their southward migration when they are blown off their route by trade winds. Because bird migratory flux is not constant, Eleonora's falcons store their prey around their nests during periods of intense migratory flux (figure 1d). We quantified the frequency of seeds in the guts of birds migrating from Europe to Sub-Saharan Africa that were blown off course towards the Canary Islands.

(b) Seed collection

The fieldwork was carried out in September 2012 and from early August to early October 2013. Most of the fieldwork was based

in Alegranza (10.5 km², 289 m.a.s.l.; $n = 312$ migratory birds), a small volcanic island situated approximately 170 km away from the African coast (27°37' N, 13°20' W; figure 1a). To increase our sample size, we also visited the nearby islands of Montaña Clara (2.7 km², 256 m.a.s.l.; $n = 30$) and Roque del Este (0.06 km², 84 m.a.s.l.; $n = 66$), which are two smaller islands that together with Alegranza make up the entire breeding area of Eleonora's falcon on the Canary Islands. Seeds were recovered from birds in migratory flight that had been hunted by Eleonora's falcons and stored around their nests. We removed the digestive tract of the stored prey birds *in situ* and then left the corpses where they were found for later consumption by the falcons. The digestive tracts were dissected, and their contents were washed out and then inspected under a stereoscope. Recovered seeds were carefully cleaned and dried, and then stored in absorbent paper at 4°C until further processing.

(c) Falcon movements

To ensure that migratory birds were hunted while in migratory flight, we identified the hunting areas of Eleonora's falcons by tracking seven different individuals with GPS trackers [23]. We tagged six adult Eleonora's falcons with solar-powered GPS trackers (www.UvA-BiTS.nl) during the breeding season of 2012 (three males and three females), and we tagged an additional falcon (female) in 2013. Four out of the six falcons tagged in 2012 returned from their wintering quarters in Madagascar in 2013; therefore, we recorded movement data from five falcons in 2013. Each geographical position was recorded at intervals ranging from 3 to 60 s with a precision of 3–15 m. These falcons leave the island to hunt rather than hunting on land. This is supported by repeated observations of falcons arriving from open sea with prey during the fieldwork and by the total absence of resident bird species from the falcons' diet (almost exclusively composed of migratory birds, plus some marine bird species). To investigate where falcons were hunting, we calculated the direction and maximum distance of falcon's movements out of a 500 m buffer around the island (to exclude casual flights near the island perimeter). We also tested whether these movements were related to the wind regime by performing an one-way ANOVA using the maximum distance as the response variable and the direction quadrant from where the wind was blowing (NE, SE, SW and NW) as a fixed independent factor. Pairwise differences in maximum distance among the different wind regimes were tested by performing post hoc Wilcoxon tests with a progressive Bonferroni correction. The predictions were that (i) falcons hunt east from the island, from where bird prey are expected to pass if migrating along the African coast, and (ii) the maximum distance decreases when winds blow from an eastern component, as eastern winds drag migratory birds closer and thus falcons can hunt near the island (i.e. maximum distance under winds blowing from NE/SE < SW/NW). Statistical analyses were performed in R [24].

(d) Seed identification

(i) DNA barcoding

We extracted DNA from the endocarp and embryo using the DNeasy Plant Kit (Qiagen, Hilden, Germany). Because a DNA barcoding protocol for plants is not fully established, we chose two commonly used DNA markers, the *matK* gene and the *rbcL* gene (subunit b; *rbcLb*), according to the CBOL Plant Working Group [25] and recent work on the efficacy of these two markers in identifying plant species [26,27]. For DNA amplification by PCR, we used pairs of primers that provided the best discriminatory power in the barcoding analyses from Yu *et al.* [27] for *matK* (forward: 5'-CCCRTYCATCTGAAATCTTGGTTC-3'; reverse: 5'-GCTRTRATAATGAGAAAGATTTCTGC-3') and Dong *et al.* [26] for *rbcLb* (forward: 5'-AGACCTTTTTGAAGAAGGTTCTGT-

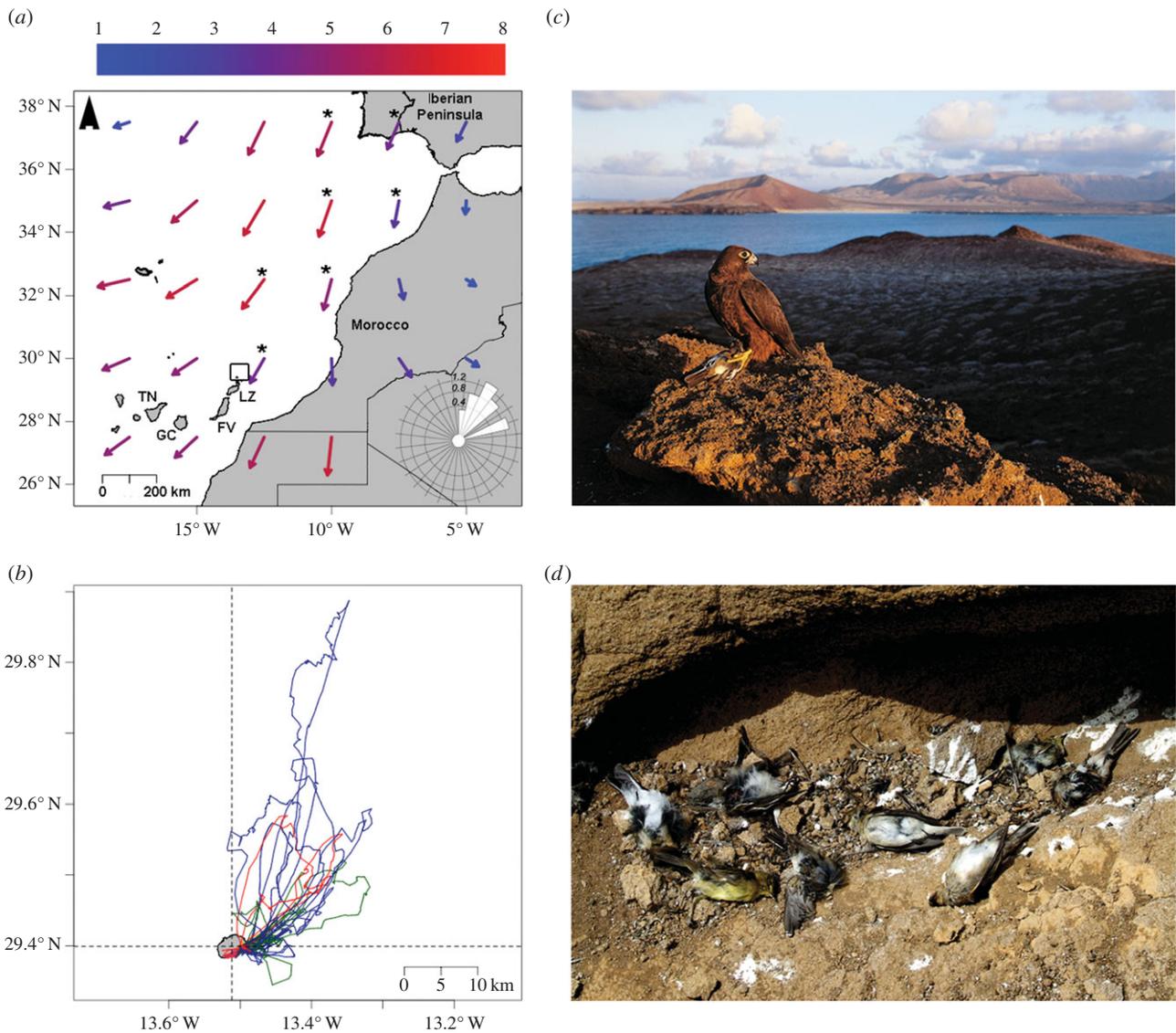


Figure 1. Wind regime and Eleonora's falcons' hunting movements. (a) Average wind direction (arrows) and speed (m s^{-1} ; represented by arrow length and colour) on days on which seeds were recovered from migratory bird prey and on each day prior, when migratory birds were also potentially migrating. The wind rose (at the bottom right) represents the circular histogram of wind direction (the direction from which it blows) and the speed corresponding to a geographical band ranging from the southern Iberian Peninsula to Alegranza (data locations indicated by asterisks; wind data were obtained from the National Centers for Environmental Prediction, NOAA). The black rectangle delimits the geographical area shown in panel (b), which includes Alegranza. TN, Tenerife; GC, Gran Canaria; FV, Fuerteventura; LZ, Lanzarote. (b) Eleonora's falcons' hunting movements (lines) during the same periods as in panel (a). Data from each individual are shown in a different colour. Alegranza is represented as a grey polygon, and the dashed lines cross its centroid and delimit its four main geographical quadrants (NE, SE, SW and NW). (c) Photograph of an Eleonora's falcon holding its bird prey in the study area (photo: J. Palmero). (d) Photograph of a typical larder where hunted migratory birds are stored.

3'; reverse: 5'- TCGGTCAGAGCAGGCATATGCCA-3'). The PCR mixture contained $1\times$ PCR buffer, 2.5 mM MgCl_2 , 0.5 mM dNTPs, 5 μg BSA, 0.25 μM of each primer, 1 U of Taq polymerase and 5–50 ng of DNA template in a total volume of 20 μl . DNA was amplified using a PCR protocol consisting of 3 min at 94°C; followed by 40 cycles of 30 s at 94°C, 40 s at 50°C for *matK* and 55°C for *rbcLb*, and 1 min at 72°C; and a final extension of 10 min at 72°C. The PCR products were then sequenced in both forward and reverse directions using the BigDYE v. 1.1 Terminator Cycle Sequencing Kit (Applied Biosystems, Inc.) and an automated DNA fragment analyser (ABI-3130xl; Applied Biosystems, Inc.). Sequences (i.e. barcodes) were visually inspected and edited using the program SEQUENCHER v. 4.9 (Gene Codes Corporation) and matched against the GenBank database (NCBI) to identify taxa with similar DNA profiles.

Barcode amplification was 100% (6/6) and 66.6% (4/6) successful for the *matK* and *rbcLb* markers, respectively (see electronic supplementary material, table S1, for details).

Nevertheless, we could not identify the different seeds to the species level, as the barcodes were either not 100% similar to published sequences (obtained from BLAST results in the GenBank) or matched more than one species (as with the *Persicaria* seeds).

(ii) Morphological identification

Because DNA barcoding did not identify the seeds to the species level, we also resorted to expert botanists and compared the collected seeds with seed image databanks (<http://www.plantatlas.eu>; <http://nt.ars-grin.gov/SeedsFruits/rptSeedsFruitsFam.cfm>; <http://www.oardc.ohio-state.edu/seedid/search.asp>). Seed morphology allowed us to further delimit the taxonomic level of some seeds (from family to genus level). In addition, morphological comparison of transported seeds with those of closely related plant species that occur in the Canary Islands (which could potentially match our identification) allowed us to exclude the

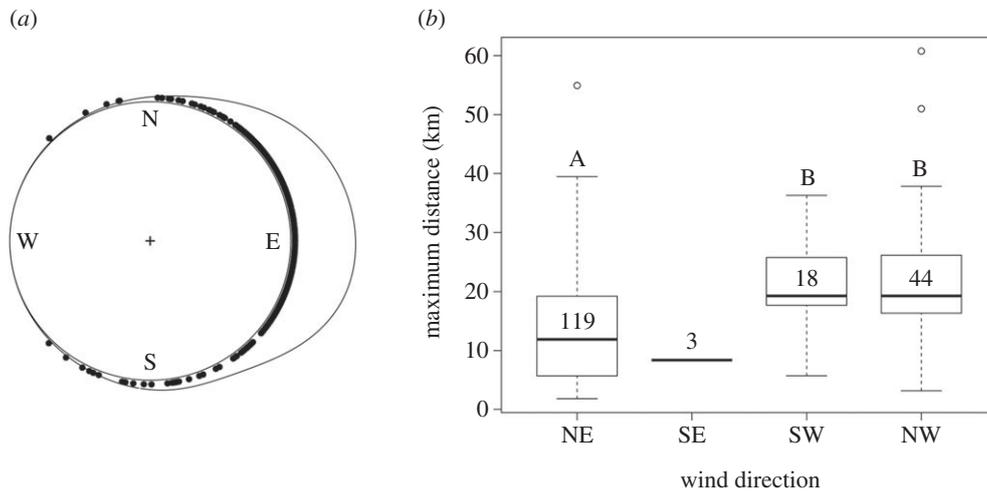


Figure 2. Hunting movements of Eleonora's falcons. (a) Direction of movements out of Alegranza (hunting incursions) and respective kernel density estimate (represented by the density line; 97% to an eastern direction). (b) Maximum distance reached in hunting incursions in relation to the wind direction (from where it was blowing). Different letters above boxplots indicate a statistically significant difference between wind regimes, and numbers inside boxes and/or above the median segments indicate the sample size (number of hunting incursions for each wind direction). The line within boxes indicates the median, the edges of the boxes the first (Q1) and third (Q3) quartiles, and the whiskers extend 1.5 times the interquartile range.

possibility of taxa originating from nearby islands or the entire archipelago (according to a recent species inventory [28]).

(e) Seed viability

The set of intact *Rubus* seeds ($n = 34$, minus one used for the DNA barcoding) recovered from one migrating quail was used to test the viability of seeds retained in a bird gut for an undetermined amount of time. The low number of remaining seeds of different species (up to 4; note that at least one seed from each taxon was used for the DNA barcoding analysis) was not sufficient to obtain reliable estimations of viability. Seed viability was assessed using the tetrazolium chloride test, which detects respiration in living tissues of the seed embryo through a chemical reaction that produces a reddish stain. The efficacy of this test using *Rubus* seeds was shown by Wada & Reed [29]. Positive and negative controls ($n = 20$ for each) were performed by testing the viability of fresh and dead seeds, respectively. The latter consisted of fresh seeds heated to 100°C for 1 h. Seeds were soaked for 24 h in water, cut longitudinally through the midsection, treated with 1% 2,3,5-triphenyl-tetrazolium chloride for 24 h at room temperature and then treated with 85% lactic acid for 30 min [29,30]. Embryos were evaluated under a stereoscope. Embryos that were entirely stained red were considered viable, whereas those that remained entirely or partially white were considered non-viable.

3. Results

On days when bird prey was found around falcon nests, winds were blowing from NE (figure 1a) and falcons travelled up to 58 km to an eastern quadrant off the island (mostly to the NE quadrant; figure 1b). Eleonora's falcons foraged every day east from the island at open ocean (97% of movements towards east; figure 2a), from where migratory birds are expected to appear. When wind was blowing from a western quadrant, they moved longer distances in search for prey when compared with eastern winds (figure 2b; $F_{2,71} = 3.601$, $p = 0.032$; post hoc tests: $p_{NE-SW} = 0.049$, $p_{NE-NW} = 0.013$, $p_{SW-NW} = 0.901$; SE direction is not compared because wind virtually never blew from SE during the study period). The contents of the digestive tracts (mostly gizzards and, when still intact,

intestines) of 408 migrating birds belonging to 21 different species were analysed (figure 1c,d). We found 45 intact seeds in the gizzards of five prey birds (1.2% of all prey birds). Common quail (*Coturnix coturnix*) was the species that transported seeds most often (three out of eight individuals, plus one individual that carried two fragments of legume loment), and did so in higher quantities (mean = 14 seeds, plus seed fragments; table 1). Viability tests (tetrazolium testing) showed that 12% of the (apparently intact) *Rubus* seeds found in a common quail were still viable, compared with 70% of control seeds collected from fresh fruits (and 0% of negative controls). Two insectivorous species, the common redstart (*Phoenicurus phoenicurus*) and the European pied flycatcher (*Ficedula hypoleuca*), transported seeds of fleshy fruits (two *Rhamnus* species) at low frequency (one bird each out of 14 and 157 birds for the common redstart and the European pied flycatcher, respectively; table 1).

Although the exact geographical origins of the seeds (belonging to four different families; table 1; see DNA barcoding results in electronic supplementary material, table S1) are not known, none of the taxa occur on the closest main island (Lanzarote), and only one taxon (*Rubus*) occurs in Fuerteventura (80 km SW; see map in figure 1a). Therefore, the nearest seed sources for most taxa are located either 170 km (in Morocco) or 230 km away (in Gran Canaria, west of Alegranza; see distance matrix in electronic supplementary material, table S2). Gran Canaria was not a likely seed source because the bird migratory flux came from the NE and not from the west (figure 1a,c; see Discussion). Further, one seed taxon (*Persicaria* sp.) does not occur on the Canary Islands; thus, these seeds must have come from the African or European continents. Migratory birds might depart from the SW Iberian Peninsula or northern Morocco, and are blown during migratory flight by strong NE winds onto the Canary Islands (figure 1).

4. Discussion

We found that 1.2% of the sampled birds carried seeds while migrating. Although five out of 408 birds transporting seeds

Table 1. Summary of the sampled digestive tracts of migratory birds hunted by Eleonora's falcons. The number of vectors is the number of birds transporting at least one seed in their gut.

bird species	no. birds	no. vectors	no. seeds	plant taxon
<i>Ficedula hypoleuca</i>	157	1	2	<i>Rhamnus</i> sp.
<i>Sylvia communis</i>	104	0	0	—
<i>Hippolais polyglotta</i>	41	0	0	—
<i>Lanius senator</i>	16	0	0	—
<i>Phoenicurus phoenicurus</i>	14	1	1	<i>Rhamnus</i> sp.
<i>Sylvia cantillans</i>	14	0	0	—
<i>Phylloscopus trochilus</i>	11	0	0	—
<i>Phylloscopus bonelli</i>	9	0	0	—
<i>Coturnix coturnix</i>	8	3	42	<i>Rubus</i> sp. Genisteeae <i>Persicaria</i> sp.
<i>Actitis hypoleucos</i>	7	0	0	—
<i>Luscinia megarhynchos</i>	6	0	0	—
<i>Muscicapa striata</i>	3	0	0	—
<i>Sylvia borin</i>	3	0	0	—
<i>Acrocephalus paludicola</i>	2	0	0	—
<i>Locustella naevia</i>	2	0	0	—
<i>Motacilla flava</i>	2	0	0	—
<i>Oenanthe oenanthe</i>	2	0	0	—
<i>Saxicola rubetra</i>	2	0	0	—
<i>Luscinia svecica</i>	1	0	0	—
<i>Oenanthe hispanica</i>	1	0	0	—
<i>Phalaropus fulicarius</i>	1	0	0	—
<i>Phylloscopus</i> sp.	1	0	0	—
<i>Sylvia</i> sp.	1	0	0	—

might seem circumstantial, it is important to consider that (i) we have found dispersed seeds during the two study years, and, (ii) although the proportion of birds transporting seeds is low, several billions of migratory birds migrate between Europe and Africa every year [31]. Consequently, our results show that migratory birds mediate regular seed dispersal, on the order of millions of seeds, over the ocean between Europe and Africa and into the Canary Islands. This study constitutes the first empirical evidence that such LDD is actually possible and quantifiable.

Aleganza is a dry volcanic island with a depauperate local flora (the typical landscape can be seen in figure 1c). All of the transported plant taxa do not occur on the island and some do not occur on nearby islands or the entire Canary Archipelago. Although propagules arrive in considerable quantities,

environmental constraints such as limited water availability may prevent successful island colonization by many transported taxa. Therefore, our results also provide a direct example of how niche processes may function as post-dispersal filters regulating species establishment. This implies that studies inferring dispersal rates from colonization patterns alone are likely to greatly underestimate the frequency of long-distance transport of propagules. Our study shows that one out of every 80 migratory birds dispersing seeds is a feasible frequency to allow the study and quantification of seed LDD in the field. Despite post-dispersal environmental filters, future studies aiming at quantifying this phenomenon may use other sampling methods, such as sampling migrating birds that fly into lighthouses or are captured by human hunters along migratory routes. Nevertheless, identifying seed sources so that dispersal distances can be calculated will be crucial for the estimation of LDD kernels and its ecological consequences. Our particular study system might also be interesting for studying potential secondary dispersal by Eleonora's falcons [32], which might ingest and disperse the seeds carried by their prey. Secondary dispersal may only occur after prey consumption, and thus before the seeds are deposited by the primary vector (i.e. the migratory bird). Given that seeds survive and are retained in the falcons' guts long enough, secondary dispersal may occur within and between islands, as well as between the Canary Islands and Africa. Note, however, that we used Eleonora's falcons as a tool to sample birds while in active migration. Most birds migrating to Africa are not hunted by falcons, and seed dispersal will occur after completion of migratory flights. Furthermore, birds completing their migratory flights will probably be more successful LDD vectors, because stopover and wintering habitats should be more suited than the studied volcanic island for the establishment of dispersed plants.

Because the transported plant taxa do not occur on Aleganza, ingested seeds could not have originated there. According to the wind patterns and the falcons' hunting areas revealed by GPS tracking in our study, migrating birds must have been caught after several hundred kilometres of non-stop flight—at least 300 km if flying from a coastal location in Morocco situated NE from Aleganza or over 1000 km if arriving from the Iberian Peninsula. Regardless of where the birds are arriving from, our results show that birds are able to initiate and maintain flight with seeds in their guts, corroborating the hypothesis that birds can transport seeds while in migratory flight. Furthermore, 12% of the *Rubus* seeds transported by a common quail were still viable, and indeed ingested seeds have been shown to survive gut passage in this bird species [33]. Also, seeds ingested by redstarts and flycatchers, which have a complementary frugivorous diet during the migration season, were shown to survive gut passage [34]. The fact that seeds survive gut passage suggests that these bird species can effectively disperse seeds and mediate the colonization of remote areas. Although viability seems to be affected by LDD (it decreased from 70 to 12% in *Rubus* seeds), it further supports that migratory birds may be responsible for the colonization of some of the Canary Islands, as many bird-dispersed plants, such as *Rubus* and *Rhamnus* species, occur on islands such as Tenerife [35]. In many other areas of the globe, the dispersal syndromes (inferred from seed or fruit characteristics) of a considerable proportion of plant species are also compatible with bird-mediated colonization (e.g. [11,36,37]). In Krakatau, for example, between 12 and 32% of the flowering plant species

that colonized the island (as by 1994) after the volcanic eruption (in 1983) have seeds adapted to ingestion by or attachment to birds [37]. Moreover, a wide array of propagules from different taxa, including cyanobacteria, lichens and plants, as well as land and aquatic invertebrates, are commonly found in either the faeces or body of vector birds (e.g. [18,19,21,38–40]). For many of these passively dispersed taxa, continental-scale dispersal mediated by birds is the only parsimonious explanation for their phylo- and biogeographic patterns, as inferred from studies on angiosperms [13,16], bryophytes [39,41], lichens [42], freshwater zooplankton [43,44] and marine snails [45]. This study constitutes a definitive proof of LDD as a biogeographic mechanism.

Quantifying LDD will allow estimating and calibrating the tail of dispersal kernels. Indeed, the LDD frequency reported here (1.2%) is within the ranges reported in a recent modelling study [10], suggesting that up to 3.5% of the propagules ingested by migratory waterbirds can be effectively dispersed over more than 100 km. The shape of these kernel tails might depend on the migratory strategy and body size of vector birds and on the geographical configuration of habitat patches used by migratory birds en route [10,46]. While migration over continental land by birds using a stepping-stone strategy might generate more continuous, fat-tailed kernels, migration over ocean or inhospitable land, as well as non-stop migrations, might generate disjunct kernels. The shape of kernel tails will ultimately contribute to explaining and predicting biogeographic patterns. For example, it might aid in resolving Reid's paradox, which, based on observed range expansion rates, predicts a higher dispersal potential than that estimated from dispersal kernels [47]. Further, incorporating LDD estimates in species distribution models will help make more realistic predictions of future species distributions.

We conclude that both omnivorous and frugivorous migratory birds can disperse seeds over hundreds of kilometres. Considering the broad distribution and high abundance of migratory birds, their LDD services can be translated into large amounts of propagules of different species travelling each year over large spatial scales, including dispersal to islands and between continents. Despite the existence of environmental filters that can hamper the establishment of long-distance dispersers, it is worth noting that recruitment

probabilities can significantly increase after arrival through directed local-scale dispersal to suitable microhabitats [48]. Our results together with this post-arrival establishment mechanism show that LDD can generate a constant propagule pressure capable of promoting and accelerating the colonization of different biogeographic regions. Depending on the LDD effectiveness, migratory birds can also promote gene flow among populations distributed along bird migration routes [43,44]. In the presence of rapid global change, LDD will allow species to rapidly reach suitable habitat patches and respond to changing environmental conditions, thus facilitating the persistence of many taxa under habitat fragmentation [9,49]. Overall, understanding and quantifying LDD by migratory birds will be necessary to estimate the potential for range adjustment in many species, including invasive species and pathogens, that are capable of exploiting these LDD vectors.

Ethics. Research permits were granted by the Spanish regional administration Consejería de Medio Ambiente, Caza y Patrimonio, Cabildo de Lanzarote (permits no. ES-000844/2012 and ES-000642/2013).

Data accessibility. All relevant data are contained within the manuscript and the electronic supplementary material.

Authors' contributions. L.G. and D.S.V. collected and analysed data; J.F., L.G. and D.S.V. designed the study; W.B. provided materials and processed the GPS data; D.S.V. wrote the manuscript. All authors discussed and commented on the manuscript and gave final approval for publication.

Competing interests. We have no competing interests.

Funding. This study was funded by the Cabildo de Lanzarote, Ministerio de Economía y Competitividad (project CGL2012-30759) and the EU project EDENext (FP7-261504). D.S.V. was supported by Fundação para a Ciência e Tecnologia grant SFRH/BD/48091/2008 and by Recupera H2020; both sources are co-financed by the European Social Fund. L.G. was supported by the Junta de Andalucía project P11-RNM-7038.

Acknowledgements. This work was made possible thanks to the help of J. J. Moreno. M. Majem, M. de la Riva, J. Rodríguez, Á. Blas, L. Soriano and G. Tejera helped in the fieldwork. We thank M. Alcaide, F. Sergio and M. Viana for discussions and reading the manuscript. J. M. Arroyo provided useful guidance on the molecular analysis, I. Martín performed the molecular analysis laboratory work, and R. Soriguer and C. Herrera kindly helped us with the taxonomic determination of seeds. We also thank the Jordan and López Arias families for providing work permits and the 'Reserva Marina de La Graciosa y de los islotes del norte de Lanzarote', MAGRAMA, for facilitating transport to the islands.

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