

Letter

Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands

The classic concept of long-distance seed dispersal

Ever since Darwin (1859), the dispersal of species from continents to oceanic islands, and between such islands, has been the subject of considerable speculation. These islands are those arising from the seafloor as a result of underwater geologic activity, typically volcanic or coralline, that have never been connected to continental land masses. In his seminal book *Dispersal of Plants Throughout the World*, Ridley (1930) collated considerable empirical evidence of long-distance dispersal (LDD) and proposed mechanisms responsible for the colonization of remote archipelagos. Later, van der Pijl (1982) summarized traits to define diaspore syndromes related to sea (hydrochory), wind (anemochory) and animal (zoochory) LDD. The latter includes endozoochory (dissemination of seeds in the disperser's gut) and epizoochory (seeds externally attached to the disperser's body).

These three keystone publications aimed to build a framework to predict dispersal based on plant and vector features and empirical studies. Darwin (1859) performed sowing experiments with some seeds dispersed externally by waterbirds, finding that they often germinated, while Ridley (1930) found different aquatic species of unrelated genera (e.g. *Juncus*, *Carex*, *Cyperus*, *Polygonum*) along banks of isolated ponds, and associated this distribution to waterbirds. Although Ridley (1930) provided no direct evidence for waterfowl dispersal, he assumed that transport of seeds in mud on birds' legs could be important for plants without special morphological adaptations for dispersal. Other botanists have since advanced this mechanism to explain the arrival to different oceanic islands of many small seeds lacking LDD adaptations. For instance, Carlquist (1967) estimated that c. 21% of plant species that have colonized Easter Island and 21% of those dispersed to the Juan Fernández archipelago did so in mud on the feet of birds because they lacked any special adaptation for LDD. Porter (1983) also argued that mud attached to animals was responsible for 42 out of 378 (11%) original dispersal events to the Galápagos. However, to our knowledge, there is limited evidence of LDD by terrestrial birds transporting seeds in their plumage or in mud on their legs and feet. Figuerola & Green (2002) reported that seeds of aquatic plants tend to be attached to the plumage of waterbirds and that transport by this means can be frequent over short distances. Our own experience in the

archipelagos of Galápagos, Canaries and Azores, where we have captured and ringed over 10 000 terrestrial birds, leads us to argue that epizoochory is extremely rare. Additional evidence suggests that this mechanism of dispersal might be largely restricted to waterbirds, which also transport seeds of wetland plants in their guts (DeVlaming & Proctor, 1968; Proctor, 1968; Brochet *et al.*, 2010).

Given the inherent difficulties in studying seed dispersal to oceanic islands, it is often impossible to reconstruct how plants reached these islands (Thornton, 2007; Gillespie *et al.*, 2012; Vargas *et al.*, in press). Distances from the mainland to such islands can range from tens of km (e.g. Canaries, \approx 100 km) to thousands of km (e.g. Galápagos, \approx 1000 km, Hawaii, \approx 4000 km), but it is expected that in all cases colonization will require mechanisms of dispersal distinct from those that enable short distance dispersal (e.g. within 1 km of a parent plant) and which have no immediate biogeographical consequences (Normand *et al.*, 2011). Our main goal here is to examine some possibly overlooked LDD mechanisms involved in seed transportation to and between oceanic islands. In doing this, we must be clear about the use of the term mechanism in contrast to syndrome, and vector of dispersal. Here, dispersal syndromes are considered to be morphological adaptations of diaspores, which increase the likelihood of their dispersal. Dispersal mechanisms are defined as typical (i.e. predictable) pathways by which seeds attain LDD, regardless of the adaptations they might possess. Finally, dispersal vectors are the actual means by which seeds are dispersed, independently of dispersal syndrome or mechanism.

Stochastic LDD mechanisms or nonstandard poorly known processes

Vegetative and reproductive parts of the plant are susceptible to be dispersed by different mechanisms, although fruits and seeds are primarily responsible for most cases of LDD colonization. When fruits and seeds are dispersed by a mechanism other than that to which they are particularly well adapted (see Ridley, 1930; van der Pijl, 1982), that is, a nonstandard dispersal mechanism (Higgins *et al.*, 2003), such events have often been classified as stochastic (Clark *et al.*, 2001). We consider as 'stochastic' those dispersal processes that are impossible to predict, for example those linked to exceptional conditions, such as storms or tsunamis. However, to dismiss such means of dispersal as attributable to chance alone might oversimplify the importance of deterministic, but poorly understood, processes. Considering the limited predictive power of morphological dispersal syndromes and the wide variety of nonstandard mechanisms (see Wilkinson, 1997; Vargas *et al.*, in press), some authors have emphasized the likely importance of stochastic LDD events (Higgins & Richardson, 1999; Higgins *et al.*, 2003; Nathan, 2006) and

pointed out the need for better empirical data relevant to such processes. Next, we enumerate some potentially important but still poorly understood mechanisms of LDD, which we regard as having been overlooked in the past (summarized in Table 1):

Dispersal by omnivorous birds

Some medium and large-sized birds, not typically frugivorous, frequently broaden their diet to include fruits/seeds of different species when these are abundant. The biogeographical importance of this in the migration of trees during the Holocene in Europe (often thought of as exclusively wind-dispersed) has been suggested by Wilkinson (1997), with birds acting as seed dispersers on large spatial and temporal scales. In an insular context, some bird species are widely distributed and have to cope with new ecological conditions for life on these islands, which frequently have a depauperate biota. Under such conditions, species have to obtain food from a wider range of sources, a phenomenon known as 'niche expansion' (Wright, 1980). This has been reported for several species of gulls on both islands (e.g. Gilham, 1952; Nogales *et al.*, 2001; Calviño-Cancela & Martín-Herrero, 2009) and continents (e.g. Ridley, 1930; Morton & Hogg, 1989; Cortés, 1994). In a recent review of frugivory and seed dispersal by gulls (Calviño-Cancela, 2011), a total of 31 species were found to disperse seeds of *c.* 100 plants worldwide, which illustrates the potential importance of this bird group as seed dispersers. Practically half of these plants produce dry fruits with most having no particular LDD syndrome, as is the case for many plants that arrive on and colonize oceanic islands (see Vargas *et al.*, in press). Gulls can move hundreds and even thousands of kilometres from their home areas (Cramp & Simmons, 1983), retaining seeds in their guts for long periods (between \approx 9.5–17 h; Nogales *et al.*, 2001). Thus, they may feasibly move seeds within their digestive tract from continents to

islands and between islands, at least within the same biogeographic region.

Besides gulls, the Corvidae (basically crows and ravens) are often reported to be seed dispersers. They are known to disperse seeds of > 30 species of gymnosperm and angiosperm species in North America (Wenny, 2001 and references therein), South America (Trucco & Caziani, 2008), Europe (Herrera, 1995; see Wilkinson, 1997), Africa (Dean & Milton, 2000) and Asia (Masaki *et al.*, 1994; Corlett, 2000). The raven (*Corvus corax*) deserves special mention in the Canary Islands, where it legitimately disperses a minimum of 15 plant species (Nogales *et al.*, 1999). Raptors may also be important as long-distance seed dispersers. In some continental areas, 13 of these bird species included in the families Cathartidae, Accipitridae and Falconidae directly consume fruits and disperse seeds of > 20 plant species (see review by Galetti & Guimaraes, 2004 and references therein). In the particular case of aquatic environments, recent studies revealed that waterbird-mediated transport of plant propagules by endozoochory is frequent (Figuerola & Green, 2002 and references therein, Sánchez *et al.*, 2006). Indeed, some waterbird species like *Charadrius vociferous* (Charadriidae) and *Erolia minutilla* (Scolopacidae) can retain viable seeds in their guts for over 1 wk and sometimes up to 2 wk, which suggests a high potential for LDD (Proctor, 1968).

Most of these avian groups show dispersal-enhancing traits for LDD, such as great capacity for seed loading owing to their relatively large body size; strong flying-power; relatively long gut-passage time; and regular spatial and temporal movements.

Legitimate dispersal by 'seed predators'

While most fleshy fruits are well adapted to promote seed dispersal by providing a nutritional reward to seed dispersers, seeds can also be important sources of energy (Norconk *et al.*, 1998).

Table 1 Summary of evidence supporting the importance of three overlooked mechanisms for long-distance seed dispersal to and between islands

Proposed mechanism	Characteristics supporting long-distance dispersal abilities	Evidence from islands
Dispersal by omnivorous birds	Great capacity for seed transportation owing to their relatively large body size Strong flying-power Relatively long gut-passage time Regular spatial and temporal movements to and between islands	Shorebirds in the Galápagos (Proctor, 1968) Ravens in the Canaries (Nogales <i>et al.</i> , 1999) Gulls in the Canaries (Nogales <i>et al.</i> , 2001) and the Atlantic islands-Galicia (Calviño-Cancela, 2011)
Legitimate dispersal by 'seed predators'	Seed predators are common and abundant in islands Diet breadth is typically broader on islands, including many fruits and seeds Many granivorous birds are regular migrants on islands	Finches in the Galápagos (Guerrero & Tye, 2009) Granivorous birds in the Azores (Heleno <i>et al.</i> , 2011) Snow buntings in Surtsey (Fridriksson, 1975)
Secondary seed dispersal (diplochory)	Predatory birds frequently eat frugivorous lizards and birds, prey that are usually abundant Predatory birds tend to have good dispersal abilities as a result of their large body size, high flying capacity, long gut-passage times and movements to and between islands Regular seasonal process	Owls and finches in the Galápagos (Grant <i>et al.</i> , 1975) Shrikes and lizards in the Canaries (Nogales <i>et al.</i> , 1998, 2007; Padilla <i>et al.</i> , in press) Kestrels and lizards in the Canaries (Nogales <i>et al.</i> , 2002, 2007; Padilla <i>et al.</i> , in press)

Many frugivores have developed morphological attributes (e.g. particularly strong beaks) or techniques that allow them to digest the seed content, taking full advantage of ingested fruits. These frugivores have been called seed predators (Janzen, 1971), seed consumers (Hampe, 2001) or granivores (Bartuszevige & Gorchov, 2006), and are generally considered to play a negligible role in the process of seed dispersal (Hampe, 2001; Herrera & Pellmyr, 2001; Hulme, 2002). However, it is now widely accepted that many animals do not strictly fit into this dichotomy of seed predators vs legitimate seed dispersers. For example, rodents, ungulates and primates which usually act as seed predators can be successful seed dispersers (e.g. Price & Jenkins, 1986; Clark *et al.*, 2001). Although to date there is a scarcity of studies quantifying this effect in birds, two recent contributions reveal that at least avian seed predators can be very successful seed dispersers in oceanic islands, particularly of small seeds. Guerrero & Tye (2009) evaluated the seed dispersal abilities of the Galápagos finches, typically considered as seed predators, and discovered that the nine species studied consume fruits, seven of them defecating viable seeds and thus implying a potential for LDD. Two species in particular (*Camarhynchus pallidus* and *Certhidea olivacea*) were basically legitimate dispersers, destroying only a small proportion of ingested seeds (Guerrero & Tye, 2009). This study dispelled the common notion that Galápagos finches are relatively unimportant for seed dispersal in the Galápagos. Likewise, a study of four granivorous bird species in the Azores showed that all were capable of dispersing intact seeds, and that one of them (*Fringilla coelebs*) was as effective in moving seeds as the most important local seed dispersers (Heleno *et al.*, 2011). So far, it is still unclear if this pattern emerges from the typically broad diet of oceanic island animals or if it is a more ubiquitous pattern. Nevertheless, there are reasons to suspect that seed dispersal by typical 'seed predator birds' might be a much more important process than was previously thought, and one that provides an alternative, nonstandard, mechanism of seed colonization to and between oceanic islands.

Secondary seed dispersal (diplochory)

Nonstandard dispersal vectors can achieve LDD of seeds in indirect ways (Vander Wall & Longland, 2004), and despite their importance (Vander Wall *et al.*, 2005), such patterns of dispersal are difficult to identify and study. For example, raptors frequently prey upon frugivorous birds, ingesting the seeds contained in their guts (Ridley, 1930). This has been shown to result in seed dispersal in continental areas (Balgooyen & Moz, 1973; Hall, 1987; Dean & Milton, 1988; Engel, 2000; Pearson & Ortega, 2001; Shanahan *et al.*, 2001). In the Canary Islands, secondary dispersal via double endozoochory also involves frugivorous lizards and their common predators (shrikes and kestrels, Nogales *et al.*, 1998, 2002, 2007), and it is feasible that this might be a common LDD mechanism in insular environments worldwide (Moore, 1999). Lizards are important frugivores in island ecosystems (see Olesen & Valido, 2003 and references therein) and shrikes and raptors are important predators of such

lizards (Martín & Lorenzo, 2001). In a recent survey in the Canary Islands, seeds of > 60 plant species (most of which were viable) were found in the pellets of shrikes and kestrels (Padilla *et al.*, in press) and discarded lizard guts (Padilla & Nogales, 2009). Other cases of secondary dispersal have probably been overlooked by ecologists because of the complexity of the mechanism. Diplochory, involving finches and owls as primary and secondary seed dispersers, respectively, has been documented for *Chamaesyce amplexicaulis* (Euphorbiaceae) in the Galápagos Islands (Grant *et al.*, 1975), and may result in seed dispersal between islands. Apart from fleshy fruits, diaspores with no morphological adaptations to increase the likelihood of dispersal (e.g. dry fruits) are often ingested by omnivorous vertebrates on islands (generally birds and reptiles), which are prey to predatory birds and thus susceptible to LDD events.

At this stage, we cannot assess how often diplochory occurs in nature and what its overall contribution is to LDD events, because it has been insufficiently studied. What is known, however, is that the mechanism involves different types of predatory birds (raptors, shrikes and herons), and that most predators move seeds longer distances than the primary dispersal vector (Higgins *et al.*, 2003). We argue here, therefore, that diplochory by double endozoochory could play a more important role in seed dispersal than is currently recognized (Nogales *et al.*, 2007). Indeed, many of these predatory birds have been recorded on oceanic islands and some are regular winter or migratory visitors to the most iconic oceanic archipelagos (e.g. Martín & Lorenzo, 2001 for the Canaries; Pyle, 2002 for Hawaii; Wiedenfeld, 2006 for the Galápagos).

Evaluating nonstandard LDD mechanisms on recent volcanic islands

Some legitimate dispersal vectors have been recorded and quantified on the recently formed volcanic islands, Surtsey (Iceland, North Atlantic Ocean) and Anak Krakatau (Indonesia, Indian Ocean) (see Thornton, 2007). However, there are marked differences between these two islands in the ways in which they have been colonized by plants and the dispersal mechanisms involved. Approx. 25 yr after the emergence of Surtsey from the seabed, 64% of the angiosperms now present on the island seem to have been brought to the island by birds, 27% by sea currents (including rafts) and 9% by wind (Fridriksson, 1992). By contrast, on Anak Krakatau it is estimated that 23% of plant species arrived through dispersal by animals (birds and bats), 55% by sea and 22% by wind (Thornton, 1992). The fact that birds seem to have played a more important role in plant colonization on Surtsey than on Anak Krakatau over an equivalent time period might be a result of the presence on Surtsey of seabird colonies (especially gulls) before it supported resident land birds, while this was not the case on Anak Krakatau (Thornton, 2002). Migratory birds (mainly frugivorous) were almost certainly involved in the colonization of Surtsey by angiosperms. Indeed, 60 out of 230 species of migrant birds observed in Iceland had been recorded on Surtsey by 1975 (Thornton, 2002), and following a population explosion in the gull colony after 1986, there was an increase in

colonization of the island by angiosperms. Additionally, some new plants were recorded under the nests of omnivores (e.g. ravens, *C. corax*) and migratory birds, such as the snow bunting (*Plectrophenax nivalis*), a presumed 'seed predator'. Indeed, a total of 87 seeds of various species were extracted from the gizzards of 32 of these birds, of which at least two plants (*Polygonum persicaria* and *Carex nigra*) germinated successfully (Fridriksson, 1975). The confirmation of these LDD events gives supporting evidence to the mechanisms we propose here.

We advocate that future research should focus on nonstandard LDD mechanisms such as those presented here, and others not yet reported, in studies of the colonization of oceanic islands by plants. The three mechanisms herein discussed require explicit testing in different oceanic archipelagos. Such research should take advantage of molecular tools that are likely to be highly effective in the study of LDD to oceanic islands (see Queiroz, 2005; Vargas, 2007 and references therein), relating genetic fingerprints of plants to source populations and migration routes.

While we have focused here on LDD events related to animal movements, other specific but still poorly known LDD mechanisms, such as anemochory (by wind) or hydrochory (by water), should also be evaluated in the context of dispersal to oceanic islands (see Gillespie *et al.*, 2012). In this way, a greater understanding will be gained of mechanisms of dispersal to oceanic islands, which in the past have been placed in the stochastic, 'black-box' drawer.

Acknowledgements

We would like to thank D. J. Crawford, H. Adersen and E. W. Schupp for their valuable comments on an earlier version of the manuscript. Furthermore, three anonymous referees and the editor, Richard Abbott, had an important input into this contribution. This study is framed within a biodiversity project in the Galápagos Islands, financed by BBVA Foundation (Spain). We also thank the Charles Darwin Foundation and the Parque Nacional de Galápagos for giving us logistic support while working there.

Manuel Nogales^{1*}, Ruben Heleno^{2,3}, Anna Traveset² and Pablo Vargas⁴

¹Island Ecology and Evolution Research Group (CSIC-IPNA), 38206 La Laguna, Tenerife, Canary Islands, Spain; ²Institut Mediterrani d'Estudis Avançats (CSIC-UIB), 07190 Esporles, Mallorca, Balearic Islands, Spain; ³Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, 3001-401 Coimbra, Portugal; ⁴Real Jardín Botánico (CSIC-RJB), 28014 Madrid, Spain
(*Author for correspondence: tel +34 629 508 735; email: mnogales@ipna.csic.es)

References

- Balgooyen TG, Moz T. 1973. Dispersal of grass-fruits – an example of endornithochory. *American Midland Naturalist* **90**: 454–455.
- Bartuszevige AM, Gorchov DL. 2006. Avian seed dispersal of an invasive shrub. *Biological Invasions* **8**: 1013–1022.
- Brochet AL, Guillemain M, Gauthier-Clerc M, Fritz H, Green AJ. 2010. Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: determinants of seed survival and influence of retention time on germinability and viability. *Aquatic Botany* **93**: 99–106.
- Calviño-Cancela M. 2011. Gulls as frugivores and seed dispersers. *Plant Ecology* **212**: 1149–1157.
- Calviño-Cancela M, Martín-Herrero J. 2009. Effectiveness of a varied assemblage of seed dispersers of a fleshy-fruited plant. *Ecology* **90**: 3503–3515.
- Carlquist S. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin Torrey Botanical Club* **94**: 129–162.
- Clark JS, Lewis M, Horvath L. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist* **157**: 537–554.
- Corlett RT. 2000. Environmental heterogeneity and species survival in degraded tropical landscapes. In: Hutchings EA, John EA, Stewart AJA, eds. *The ecological consequences of environmental heterogeneity*. Oxford, UK: Blackwell Sciences, 333–355.
- Cortés J. 1994. The dragon tree *Dracaena draco* L. naturalised in Gibraltar. *Revista de Estudios Campogibraltareños* **11**: 183–189.
- Cramp S, Simmons KEL. 1983. *The birds of the western Palearctic. vol III*. Oxford, UK: Oxford University Press.
- Darwin CR. 1859. *On the origin of species*. London, UK: John Murray.
- Dean WRJ, Milton SJ. 1988. Dispersal of seeds by raptors. *African Journal of Ecology* **26**: 173–176.
- Dean WRJ, Milton SJ. 2000. Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments* **45**: 305–314.
- DeVlaming V, Proctor VW. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. *American Journal of Botany* **55**: 20–26.
- Engel TR. 2000. *Seed dispersal and forest regeneration in a tropical biocenosis Shimba Hills, Kenya*. Berlin, Germany: Logos Verlag.
- Figuerola J, Green AJ. 2002. How frequent is external transport of seeds and invertebrate eggs by waterbirds? A study in Doñana, SW Spain. *Archiv für Hydrobiologie* **155**: 557–565.
- Fridriksson S. 1975. *Surtsey: evolution of life on a volcanic island*. London, UK: Butterworths.
- Fridriksson S. 1992. Development of the ecosystem on Surtsey with references to Anak Krakatau. *GeoJournal* **28**: 287–291.
- Galetti M, Guimaraes PR. 2004. Seed dispersal of *Attalea phalerata* Palmae by Crested caracaras *Caracara plancus* in the Pantanal and a review of frugivory by raptors. *Ararajuba* **12**: 59–61.
- Gilham ME. 1952. The distribution of seeds by gulls. *Skokholm Birds Observatory Report* **1952**: 34–35.
- Grant PR, Smith NM, Grant BR, Abbott IJ, Abbott LK. 1975. Finch numbers, owl predation and plant dispersal on Isla Daphne Major, Galápagos. *Oecologia* **19**: 239–257.
- Guerrero AM, Tye A. 2009. Darwin's Finches as seed predators and dispersers. *The Wilson Journal of Ornithology* **121**: 752–764.
- Guillespie RG, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK. 2012. Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution* **27**: 47–56.
- Hall G. 1987. Seed dispersal by birds of prey. *Zimbabwe Science News* **21**: 1–2.
- Hampe A. 2001. The role of fruit diet within a temperate breeding bird community in southern Spain. *Bird Study* **48**: 116–123.
- Heleno RH, Ross G, Everard A, Memmot J, Ramos J. 2011. On the role of avian seed predators as seed dispersers. *Ibis* **153**: 199–203.
- Herrera C, Pellmyr O. 2001. *Plant–animal interactions*. Oxford, UK: Blackwell Science.
- Herrera CM. 1995. Plant-vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary and historical determinants. *Annual Review of Ecology and Systematics* **26**: 705–727.
- Higgins SI, Nathan R, Cain ML. 2003. Are long-distance dispersal events in plants usually caused by non-standard means of dispersal? *Ecology* **84**: 1945–1956.

- Higgins SI, Richardson DM. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist* 153: 464–475.
- Hulme P. 2002. Seed eaters: seed dispersal, destruction, and demography. In: Levey D, Silva WR, Galetti M, eds. *Seed dispersal and frugivory: ecology, evolution and conservation*. New York, USA: CABI Publishing, 257–273.
- Janzen DH. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2: 465–492.
- Martín A, Lorenzo JA. 2001. *Aves del archipiélago canario*. La Laguna, Spain: Francisco Lemus Editor.
- Masaki T, Kominami Y, Nakashizuka T. 1994. Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. *Ecology* 75: 1903–1910.
- Moore P. 1999. A shrike for mobility. *Nature* 379: 22–23.
- Morton JK, Hogg EH. 1989. Biogeography of island floras in the Great Lakes. II. Plant dispersal. *Canadian Journal of Botany* 67: 1803–1820.
- Nathan R. 2006. Long-distance dispersal of plants. *Science* 313: 786–788.
- Nogales M, Delgado JD, Medina FM. 1998. Shrikes, lizards and *Lycium intricatum* Solanaceae fruits: a case of indirect seed dispersal on an oceanic island Alegranza, Canaries. *Journal of Ecology* 86: 866–871.
- Nogales M, Hernández EC, Valdés F. 1999. Seed dispersal by common ravens *Corvus corax* among island habitats Canarian Archipelago. *Écoscience* 6: 56–61.
- Nogales M, Medina FM, Quilis V, González-Rodríguez M. 2001. Ecological and biogeographical implications of Yellow-Legged Gulls *Larus cachinnans* Pallas as seed dispersers of *Rubia fruticosa* Ait. Rubiaceae in the Canary Islands. *Journal of Biogeography* 28: 1137–1145.
- Nogales M, Padilla DP, Nieves C, Illera JC, Traveset A. 2007. Secondary seed dispersal systems, frugivorous lizards and predatory birds in insular volcanic badlands. *Journal of Ecology* 95: 1394–1403.
- Nogales M, Quilis V, Medina FM, Mora JL, Trigo LS. 2002. Are predatory birds effective secondary seed dispersers? *Biological Journal of the Linnean Society* 75: 345–352.
- Norconk MA, Grafton BW, Conklin-Brittain NL. 1998. Seed dispersal by neotropical seed predators. *American Journal of Primatology* 45: 103–126.
- Normand S, Ricklefs RE, Skov F, Bladt J, Tackenberg O, Svenning J-C. 2011. Postglaciation migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B: Biological Sciences* 278: 3644–3653.
- Olesen J, Valido A. 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Tree* 18: 177–181.
- Padilla DP, González-Castro A, Nogales M. (in press). Significance and extent of secondary seed dispersal by predatory birds on oceanic islands: the case of the Canary archipelago. *Journal of Ecology*. doi: 10.1111/j1365-2745.2011.01924.x
- Padilla DP, Nogales M. 2009. Behavior of kestrels feeding on frugivorous lizards: implications for secondary seed dispersal. *Behavioral Ecology* 20: 872–877.
- Pearson DE, Ortega YK. 2001. Evidence of an indirect dispersal pathway for Spotted Knapweed, *Centaurea maculosa*, seeds, via Deer Kice, *Peromyscus maniculatus*, and Great Horned Owls, *Bubo virginianus*. *Canadian Field Naturalist* 115: 354.
- van der Pijl L. 1982. *Principles of dispersal in higher plants*. Berlin, Germany: Springer Verlag.
- Porter DM. 1983. Vascular plants of the Galapagos: origins and dispersal. In: Bowman RI, Berson M, Leviton AE, eds. *Galapagos organisms*. San Francisco, CA, USA: AAAS, 33–96.
- Price MV, Jenkins SH. 1986. Rodents as seed consumers and dispersers. In: Murray D, ed. *Seed dispersal*. Sydney, Australia: Academic Press, 191–235.
- Proctor VW. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. *Science* 160: 321–322.
- Pyle RL. 2002. Checklist of the birds of Hawaii. *Elapaio* 62: 137–148.
- Queiroz A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution* 20: 68–73.
- Ridley HN. 1930. *The dispersal of plants throughout the world*. Ashford, UK: Reeve & Co.
- Sánchez MI, Green AJ, Castellanos EM. 2006. Internal transport of seeds by migratory waders in the Odiel Marshes, South-west Spain: consequences for long-distance dispersal. *Journal of Avian Biology* 37: 201–206.
- Shanahan M, So S, Compton SG, Corlett R. 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76: 529–572.
- Thornton I. 1992. Krakatau: a century of change. *GeoJournal* 28: 81–302.
- Thornton I. 2002. How important were stepping stones in the colonization of Krakatau? *Biological Journal of the Linnean Society* 77: 275–317.
- Thornton I. 2007. *Island colonization. The origin and development of island communities*. Cambridge, UK: Cambridge University Press.
- Trucco CE, Caziani SM. 2008. Remoción de semillas en un borde inducido por un incendio forestal en el chaco semiárido argentino. *Ecosistemas* 17: 123–133.
- Vander Wall SB, Kuhn KM, Beck MJ. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86: 801–806.
- Vander Wall SB, Longland WS. 2004. Diplochory: are two seed dispersers better than one? *Tree* 19: 155–161.
- Vargas P. 2007. Are Macaronesian islands refugia of relict plant lineages?: a molecular survey. In: Weiss SJ, Ferrand N, eds. *Phylogeography in southern European refugia: evolutionary perspectives on the origins and conservation of European biodiversity*. Dordrecht, the Netherlands: Springer, 297–314.
- Vargas P, Heleno RH, Traveset A, Nogales M. (in press). Success of plant colonization in the Galápagos Islands despite the absence of special dispersal mechanisms: a new perspective. *Ecography*. doi: 10.1111/j.1600-0587.2011.06980.x
- Wenny DG. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51–74.
- Wiedenfeld DA. 2006. The avifauna of the Galapagos Islands, Ecuador. *Checklist* 2: 1–27.
- Wilkinson DM. 1997. Plant colonization: are wind dispersed seeds really dispersed by birds at larger spatial and temporal scales? *Journal of Biogeography* 24: 61–65.
- Wright SJ. 1980. Density compensation in island avifaunas. *Oecologia* 45: 385–389.

Key words: biogeography, colonization, granivores, insular environments, long-distance dispersal (LDD), omnivorous birds, secondary seed dispersal, vertebrates.