

3 The Ecology of Seed Dispersal

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Introduction

Seed dispersal is one of the key phases in the regeneration process of plant populations. It determines the potential area of recruitment and, simultaneously, acts as a template for the subsequent stages of plant growth. Seed dispersal is the most common means for plants to colonize new areas and to avoid sibling competition and natural enemies such as herbivores or pathogens. Seeds can be dispersed by wind, water, gravity and by a wide assemblage of animals (including those that consume fruits and/or seeds as well as those that move seeds via their fur, plumage or feet). By directly dispersing seeds to favourable recruitment sites (Wenny and Levey, 1998) or by virtue of the treatment offered to ingested seeds (Verdú and Traveset, 2004; Traveset *et al.*, 2007), animals actually play an important role as seed dispersers for most (60–80%) plant species (Levey *et al.*, 2002; Dennis *et al.*, 2007). Moreover, seed dispersers are crucial in plant-community dynamics in many ecosystems around the globe and contribute to numerous ecosystem services offered by forests, including fruit, wood and non-timber products, carbon sequestration and forest cover – at no cost to humans (Forget *et al.*, 2011).

Seed dispersal is currently a very active research area that includes both ecological and evolutionary aspects. Studies have diversified in the last few decades mainly towards the study of landscape ecology (movement patterns), plant genetic diversity and structure (gene flow through pollen and/or seeds), community ecology (e.g. mutualistic interaction networks), dispersal adaptations of both plants and seed dispersers, conservation biology (effects of different types of disturbances such as habitat fragmentation, defaunation and biological invasions) and ecological restoration. Research on seed dispersal has actually shifted from being organism oriented towards being currently more mechanism oriented in order to unravel the mechanistic processes behind seed dispersal (Jordano *et al.*, 2011). Thus, for instance, by means of increasingly precise tools, such as radio or satellite tracking, researchers can now study the movement of animal seed dispersers across habitats (Blake *et al.*, 2012), or even across continents (Kays *et al.*, 2011), and evaluate plant seed dispersal kernels (i.e. the probability density function of the dispersal distance for an individual or population). Physiological, chemical and morphological mechanisms,

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of both fruits/seeds (e.g. odour, colour, shape, presence of secondary metabolites) and frugivores (e.g. digestive physiology, foraging behaviour) are also being examined in order to provide insights into the evolution of fruit displays and animal frugivory. One of the most promising fields in seed dispersal research is the estimation of dispersal kernels by using a multidisciplinary approach that combines high-resolution tracking of frugivore movements, mechanistic models of fruit processing and seed dissemination with genetic data (DNA polymorphisms) (see Jordano *et al.*, 2007; Jones and Muller-Landau, 2008).

Although most information available is from continental systems, an increasing number of studies are being carried out on islands. Insular ecosystems can be considered as natural laboratories for the evolution of dispersal adaptations. Here, frugivore assemblages are less diverse than on the continents and often unique, especially on oceanic islands, where reptiles (lizards, iguanas and tortoises), bats and pigeons play an important role as seed dispersers (Olesen and Valido, 2004; Nogales *et al.*, 2012). However, islands are highly vulnerable to disturbances and most mutualistic disruptions have actually been reported in such insular systems (Traveset and Richardson, 2006). Current studies are being performed to assess how alien species can replace extinct disperser taxa and restore lost ecosystem functions (Foster and Robinson, 2007; Hansen *et al.*, 2010).

The goal of this chapter is to review the existing literature on seed dispersal, highlighting the essential findings so far, as well as the missing gaps of information. We first review the determinants of seed dispersal, examining the main dispersal vectors, and what determines when and where seeds are moved. Next we deal with the consequences of seed dispersal right from plant genetic structure to global biogeography, passing by the population and community levels. In the following section, we focus on the causes and risks of seed dispersal disruptions for conservation and their implications for ecological restoration. Finally, we suggest directions for future studies that we believe will contribute to deepening the understanding of this crucial phase in plant

regeneration and to its integration with other disciplines in the quest to comprehend ecosystem functioning.

The Determinants of Seed Dispersal

Seeds are highly specialized structures, which greatly increase plant success by conferring their offspring a higher probability of finding suitable recruiting sites (Howe and Smallwood, 1982). This selective pressure favours seeds that are particularly well equipped for dispersal, resulting in the vast array of elaborate solutions we see today, including plumes, hairs, wings, floating devices, nutritive tissues, sticky surfaces, hooks, etc. Nevertheless, the fate of seeds is far from certain, and the journey of seeds from when they leave the mother plant until recruitment, if achieved, can be highly eventful. Such a journey is dependent on a wide variety of factors which together will determine how, when, where, by whom and if seeds will ever be dispersed and given the chance to become established adults.

How are seeds dispersed?

The presence of numerous mechanisms of seed dispersal in nature suggests that these are well adapted to enhance dispersal (Ridley, 1930; Van der Pijl, 1982). Thus, different structures are easily interpretable in terms of favouring a certain dispersal mode (i.e. dispersal syndromes), such as the presence of flotation devices to travel by oceanic currents or rivers, diaspores with wings or plumes capable of being dispersed by air, explosive opening of fruits that project their own seeds, seeds with hooks or sticky surfaces able to hitchhike on the fur of mammals, or seeds with a nutritive reward that attract foraging animals which in turn transport the seeds in their gut. Regarding animals, most seeds are dispersed by three classes of vertebrates: birds, mammals (including humans) and reptiles. Other dispersing agents can however be quite active seed dispersers, such as ants, fish, amphibians, grasshoppers, beetles, slugs,

bees and even earthworms (see Chapter 2, this volume). The relative importance of all these dispersers varies greatly according to the species of seed, but also with the local distribution, abundance and behaviour of the disperser (Fig. 3.1). More globally, the importance of the different disperser guilds varies according to the latitude and type of ecosystem; birds and mammals being crucial in temperate environments (Herrera, 1995), while reptiles take on a more important role in subtropical and tropical islands (Olesen and Valido, 2003; Nogales *et al.*, 2005) where large mammals are usually absent (Williamson, 1983; Whittaker and Fernández-Palacios, 2007) (see Box 3.1). Distinct habitats may also be related to certain dispersal mechanisms such as the high proportion of vertebrate-dispersed seeds in tropical wet forests (Willson *et al.*, 1989), and the high frequency of ant-dispersed species in sclerophyllous biomes in the southern hemisphere (Rice and Westoby, 1986). Furthermore, external dispersal on vertebrates seems to be more common along riparian corridors in arid parts of southern Africa (Sorensen, 1986).

Although morphological adaptations unequivocally increase the probability of dispersal by a certain mechanism, this does not mean that seeds cannot be dispersed by other vectors for which they are not particularly adapted (Higgins *et al.*, 2003b). Similarly, many species have simple seeds that have not developed any specific adaptation for dispersal – ‘unassisted seeds’ – which does not preclude these seeds being successfully dispersed (Cain *et al.*, 1998). An illustrative example of this potential is the proportion of plants with such ‘unassisted’ diaspores that arrived by natural means and colonized even highly remote archipelagos such as the Galápagos (Vargas *et al.*, 2012).

The different modes of dispersal generate a great variation in the dispersal potential of plants and in the relationship between dispersal mode and seed mass. This is especially evident in the genus *Pinus*; pine seeds weighing less than *c.*100 mg tend to be wind dispersed whereas heavier seeds usually have developed adaptations for bird dispersal (Benkman, 1995). Also, the size and chemical composition of the edible

appendage on ant-dispersed seeds influences the rate of seed removal, the array of dispersing ant species, and consequently the pattern of dispersal and the eventual fate of the seeds (Gorb and Gorb, 1995; Mark and Olesen, 1996). Even closely related species can display very different adaptations for dispersal. One of the most illustrative examples is found in the widely spread genus *Acacia*, with Australian species exhibiting morphological adaptations for dispersal by ants or birds (Willson *et al.*, 1989), American species adapted to dispersal by birds and/or large mammals (O’Dowd and Gill, 1986), and African species mostly adapted to dispersal by large mammals (Dudley, 1999).

Seed size is another important factor that influences the seed dispersal mode (Westoby *et al.*, 1996). Intuitively, larger seeds are generally more limited in terms of dispersal than smaller ones, because they cannot be dispersed by mechanisms such as ballistochory or by adhering to the animal exterior, and must be disseminated by larger animals, or less commonly by water currents and gravity (Foster and Janson, 1985; Wheelwright, 1985).

Plant habit also differentially affects the efficiency of particular dispersal mechanisms and therefore seed dispersal syndromes are frequently related to plant growth form. For example, the seeds of high trees are more frequently adapted to wind dispersal, while small plants may more often use ballistic mechanisms (Thompson and Rabinowitz, 1989; Willson *et al.*, 1990).

So far we have considered seed dispersal as a one-way ticket, however one seed can be transported sequentially by several processes, which can greatly affect the final outcome – a phenomenon named diplochory or secondary seed dispersal (reviewed in Vander Wall and Longland, 2004) (Fig. 3.2). Although diplochory is considerably less well studied than ‘traditional’ single-vector dispersal, due to the understandable logistical challenges, it is likely to be essential in the reproduction of some plants (Chambers and Macmahon, 1994). Secondary seed dispersal systems are widely variable because they depend on the potential combinations



Fig. 3.1. Different stages of the seed dispersal process. (a) A seed of *Ipomoea pes-caprae* recruiting in a Galápagos beach after having been dispersed by thalassochory (oceanic drift). (b) The anemochorous seeds of *Asclepias curassavica* ready for being dispersed by wind. (c) The Canarian lizard (*Gallotia galloti*) dispersing the seeds of *Rubia fruticosa* in the Canary Islands. (d) A Southern grey shrike (*Lanius meridionalis*) preying upon a frugivorous lizard (*G. galloti*) and acting as a secondary dispersal for the seeds in its gut. (e) Seeds of the tree *Hippomane mancinella* recruiting in a dung pile of the Galápagos giant tortoise (*Chelonoidis nigra*). (f) The blue tit (*Cyanistes teneriffae*), an essentially insectivorous bird, consuming and dispersing the seeds of *Opuntia maxima*. (g) The granivorous large beak ground finch (*Geospiza magnirostris*) handling and dispersing the hard seed of *Cordia lutea*. Photo credits: (a), (b), (e), (g) – Ruben Heleno; (c) – Beneharo Rodríguez; (d) – Gustavo Peña; (f) – José Juan Hernández.

Box 3.1. Seed dispersal on islands: main differences with mainland environments

The composition of island biota is the reflection of biogeographical, ecological and evolutionary processes that have simultaneously occurred since their formation (see Whittaker and Fernández-Palacios, 2007 and references therein). These insular communities are frequently considered disharmonic in relation to the species composition of the mainland source(s) due to the differential colonization capacity of organisms, often expressed in the different composition of plant families (Gulick, 1932). They are characterized by a low diversity of plants and animals, a high proportion of endemic species – especially oceanic islands – and the presence of relict species (i.e. ancient evolutionary lineages) (Carlquist, 1974). Therefore, the new species that reach and become established on islands clearly force a new order of interactions, which are particular with respect to mainland environments.

While birds and mammals are the most common dispersers of fleshy-fruited plants in mainland ecosystems, in many tropical and subtropical oceanic islands (the most biodiverse), birds and reptiles play a more determinant role (Nogales *et al.*, 2005). The community of seed dispersers on islands is often characterized by the absence of medium and large mammals, except for some large bats, and the existence of ‘unusual’ dispersers, which include a large array of reptiles such as tortoises, iguanas and lizards (Olesen and Valido, 2003; McConkey and Drake, 2006, 2007; Whittaker and Fernández-Palacios, 2007; Blake *et al.*, 2012).

At the biogeographical and ecological levels, this insular scenario promotes the emergence of unusual interactions, which are more frequent on islands than in mainland areas. Some of these interactions involve: (i) large omnivorous birds (e.g. gulls or corvids), not typically frugivorous, which frequently broaden their diet – a phenomenon known as niche expansion on islands (Wright, 1980) – and include fleshy fruits, acting as potentially long-distance dispersers (Nogales *et al.*, 1999, 2001); (ii) ‘seed predator birds’ which are often found to be legitimate seed dispersers (Guerrero and Tye, 2009; Heleno *et al.*, 2011; Young *et al.*, 2012); and (iii) predatory birds which may frequently act as secondary seed dispersers when preying upon frugivorous lizards and birds (Nogales *et al.*, 1998, 2007; Padilla *et al.*, 2012). When fruits and seeds are dispersed by a mechanism other than that to which they are particularly well adapted, i.e. a non-standard dispersal mechanism (Higgins *et al.*, 2003b), such events have often been classified as stochastic (e.g. Clark *et al.*, 2001). However, dismissing such means of dispersal as attributable to chance alone might oversimplify the importance of deterministic, but poorly understood, processes. Such ‘stochastic’ mechanisms might actually acquire a major biogeographical and ecological importance if they occurred regularly and in a number of oceanic archipelagos (Nogales *et al.*, 2012). However, despite many of these dispersal mechanisms involving regular events repeated year after year, our knowledge to evaluate their real importance in the context of islands worldwide is still incomplete.

In recent years, the use of interaction networks has grown popular as a framework to compare community structure and function (see Box 3.2, this chapter). Some general differences have been identified between mainland and island pollination networks (Olesen and Jordano, 2002), but sufficient data are so far lacking to permit generalizations about differences in seed dispersal networks. The first study comparing the structure of seed dispersal networks between island and mainland habitats has been made by González-Castro *et al.* (2012). This compares the same types of habitat (Mediterranean shrublands) in the Canary and Balearic Islands with those on the European continent (Southern Iberian Peninsula); studying the same types of habitat better allows us to infer differences due to the insularity effect. Results show that island networks are smaller (less diverse), more highly connected, and have a more asymmetric proportion of plant/animal species and a lower relative nestedness. The lower species richness and higher specialization on islands appear to promote the prevalence of more symmetric interaction frequencies than those found on the mainland (see also Box 3.2, this chapter).

of many possible abiotic and biotic dispersal agents. In some cases, the first dispersal phase is mediated by an abiotic mechanism (e.g. wind or water) whilst the second is

mediated by scatter-hoarding vertebrates (Vander Wall, 2002) or invertebrates (Pizo *et al.*, 2005). In other cases, primary seed dispersal includes a first process of endozoochory

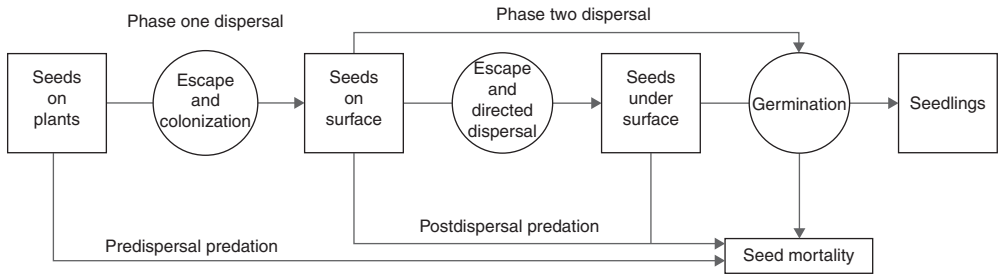


Fig. 3.2. The potential benefits of diplochory and the possible fate of seeds from when they are produced until they die or otherwise germinate and establish as seedlings. Rectangles represent physical states whereas circles symbolize the most important advantages resulting from seed dispersal. (From Vander Wall and Longland, 2004.)

(involving mammals or birds) followed by secondary dispersal by invertebrates such as ants (Christianini and Oliveira, 2010) or beetles (Santos-Heredia *et al.*, 2010).

A special type of diplochory occurs when predatory vertebrates prey upon frugivores that have recently consumed fruits, ingesting the entire seed load contained within the digestive tract of their prey. Although this phenomenon has been described for some time (Damstra, 1986), only a few studies have assessed its importance in an ecological context (Nogales *et al.*, 1998, 2007). In the Canary archipelago, for instance, this process appears to be highly important, involving a total of 78 plant species found in shrike (*Lanius meridionalis*) and kestrel (*Falco tinnunculus*) pellets (Padilla *et al.*, 2012). The large number of seeds achieving dispersal by this secondary mechanism suggests that even if representing a non-standard dispersal mechanism, it can be ecologically significant for increasing the dispersal distance of many native and endemic insular plants. While such dispersal by two vertebrate systems is likely to also occur on continents, it is not as generalized as the secondary dispersal due to a conjunction of abiotic and biotic vectors.

When are seeds dispersed?

Dispersal phenology is influenced by several ecological factors. From the plant's viewpoint, fruit development and seed

maturation should be timed to match with the seasonal availability of legitimate dispersal agents and suitable environmental conditions for dispersal and plant establishment. Some authors argue that differences in flowering phenology of tropical forests are primarily caused by abiotic factors (e.g. climatic: water or light), whereas differences in fruiting phenology are mostly influenced by biotic ones (e.g. presence of seed dispersers) (Thies and Kalko, 2004); however, few clear general patterns have emerged so far. Furthermore, wind-dispersed neotropical trees often release their seeds during the dry season, when trade winds are stronger and trees are leafless (Foster, 1982; Morellato and Leitão, 1996), while zoochorous dispersal usually occurs during the rainy season (Griz and Machado, 2001). Fleshy fruits in northern temperate latitudes mature during the late summer and autumn, coinciding with a high abundance of frugivorous birds (Willson and Thompson, 1982; Snow and Snow, 1988). On the other hand, in southern temperate latitudes fleshy fruits mature in winter, coinciding with the presence of foraging flocks of migrant birds (Herrera, 1995). While in many areas fruit and bird phenology tend to coincide (de Castro *et al.*, 2012), wide-ranging plant species show no latitudinal shift in fruiting times, as would be expected if their fruiting seasons were 'adapted' to disperser timing (Willson and Whelan, 1993); thus, patterns may not always be entirely interpretable.

Where are seeds dispersed?

The spatial distribution of seeds with respect to their source plant is called the seed shadow (Janzen, 1971); it marks the end of the dispersal stage and sets the template for future processes that might eventually lead to plant recruitment. This simple descriptor of shape is generally augmented by information on seed density per distance class, forming the dispersal kernel. Although directionality is frequently asymmetric in respect to the source and clearly significant for many ecological questions (Cain *et al.*, 2000), it is usual to discuss seed distributions chiefly in terms of the relationship between seed density and distance from the source (i.e. dispersal curve). The majority of studies of dispersal curves fit a unimodal leptokurtic distribution (with a higher peak and a longer 'fatter' tail than a normal distribution) (Willson, 1993; Kot *et al.*, 1996). However, dispersal curves can form any kind of distribution, including multimodal distributions (Schupp, 1993). Different species of dispersers generate characteristic seed shadows, depending on foraging behaviour, seed retention times, secondary seed dispersal, patterns of fruit selection and disperser responses to vegetation structure and other ecological cues (Herrera, 1995; Borges *et al.*, 2011; Guttal *et al.*, 2011). Yet other factors which determine the final shape of the seed shadow are climatic, e.g. wind, rainfall or humidity, and intrinsic characteristics of the mother plant, e.g. height, ballistic mechanisms and of course diaspore morphology.

While wind-dispersed seeds can travel remarkable distances (Nathan *et al.*, 2002), on average it seems that animal-dispersed seeds travel longer distances (Clark *et al.*, 2005). Regarding animal-dispersed seeds, different vertebrates (e.g. birds and bats), produce different seed shadows; for example, Thomas *et al.* (1988) described that birds generated a strongly skewed seed shadow towards open savanna, while bats produced a similar-shaped shadow but oriented to the nearest forest edge.

A critical component of the seed shadow is its size, which is determined by the maximum travelling distance of seeds. Because

such long-distance dispersal events tend to be rare, they are increasingly difficult to study. Different methods have been applied to study long-distance dispersal such as mechanistic models, often used in wind-dispersal systems (e.g. Nathan and Muller-Landau, 2000; Katul *et al.*, 2005; Nathan *et al.*, 2011), or more recently, genetic methods have become a highly active and diverse field of research including assignment likelihood, genealogical and demographic methods (e.g. Godoy and Jordano, 2001; Jordano *et al.*, 2007; Jones and Muller-Landau, 2008) (see Fig. 3.3). Such methods point to a close relationship between the frequency of long-distance dispersal events and the amount of genetic diversity preserved during colonization (Bialozyt *et al.*, 2006).

Mechanistic models in wind dispersal applied in open habitats indicate that auto-correlated turbulent fluctuations in vertical wind speed are key factors for long-distance dispersal (LDD) (Tackenberg, 2003; Soons *et al.*, 2004). However, abscission is often controlled by horizontal wind speed and therefore this is another important factor that needs to be successfully modelled (Greene, 2005). With regards to the plant biotype, windy and stormy weather conditions are of much less overall importance in non-tree species (Tackenberg, 2003). However, according to this last author, the number of seeds dispersed on a long-distance scale is not correlated to horizontal wind speed but to the frequency of updrafts (especially thermals). Wind dispersal distances are increased for lighter seeds and probably more importantly by plant height (Thomson *et al.*, 2011).

Animal seed-dispersal events are often grouped into loose categories regarding the distance travelled by seeds, such as short-, medium- and long-distance seed dispersal. However, no general scale has yet been proposed that can be applied more consistently across studies. While it is clear that each system requires its own ecological interpretation of dispersal distances, we consider that it is useful to define some guiding classes in order to facilitate inter-study comparisons. According to published information we suggest the following categories: (i) short-distance dispersal

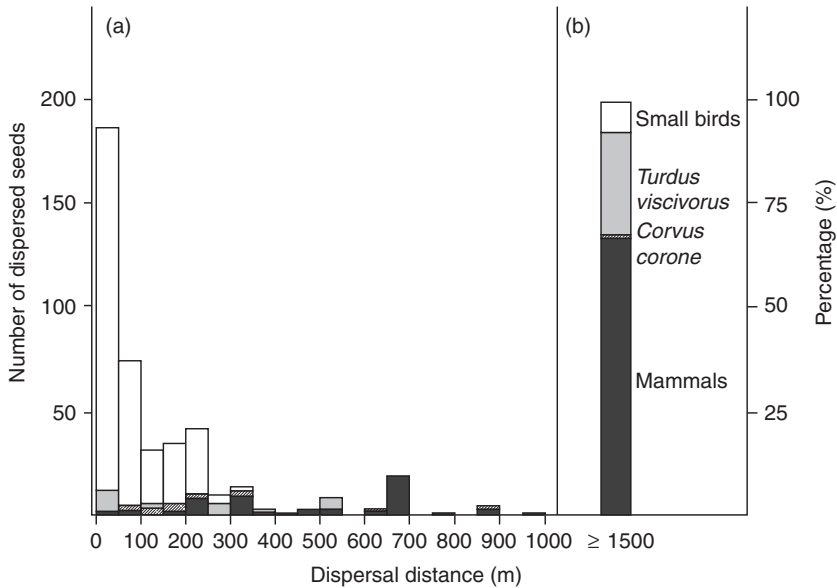


Fig. 3.3. Seed dispersal kernel of the tree *Prunus mahaleb* in Southern Spain. (a) Shows the relative contribution of major disperser guilds to different distance classes. Open bars, small- to medium-sized frugivorous birds; light grey, *Turdus viscivorus*; dark grey, *Corvus corone*; black, carnivorous mammals. (b) Shows the weighted contribution of each dispersal guild to seed immigration to the study population (dispersal distances $\geq 1,500$ m). (From Jordano *et al.*, 2007.)

(SDD) when seeds travel less than 25 m; (ii) medium-distance dispersal (MDD), from 25 m to 250 m; (iii) long-distance dispersal (LDD), from 250 m to 10,000 m; and (iv) very long-distance dispersal (VLDD), for distances over 10,000 m. Although these categories are useful as a first approximation, we envisage that a careful analysis of dispersal distances by different animal groups will help to increase precision in the limits of each category. Precise distances currently obtained by means of molecular analysis and radio and satellite tracking will help this purpose. Such an analysis will allow a better understanding of the spatial scale at which different disperser guilds disperse seeds, and evaluate the relationship between dispersers' body size and dispersal distances.

Most precise assessments of long-distance dispersal, including considerations on animal movement and retention times, have been measured in birds and mammals (Guttal *et al.*, 2011). Levey *et al.* (2008) modelled seed dispersal by terrestrial

birds and showed that the dispersal kernel was uniform in homogeneous landscapes and irregular in heterogeneous ones. In both environments, dispersal distances >150 m made up *c.*50% of all dispersal events. Gómez (2003) recorded dispersal distances of over 250 m, and up to 1 km for *Quercus ilex* acorns dispersed by Eurasian jays. In this respect, some of the long-distance movements for a large avian frugivore were up to 290 km recorded for rainforest hornbills in Cameroon (Holbrook *et al.*, 2002). Based on DNA-genotyping techniques on *Prunus mahaleb*, Jordano *et al.* (2007) recorded that small passerines dispersed most seeds over short distances (50% dispersed <51 m from source trees), while mammals and medium-sized birds dispersed seeds over long distances (50% of mammals: <495 m, and 50% of medium-sized birds: <110 m) (Fig. 3.3). In some Amazonian fish (*Colossoma macropomum*), at least 5% of seeds are estimated to be dispersed around 1700–2110 m (Anderson *et al.*, 2011).

Most of our knowledge on animal seed dispersal is focused on the internal dispersal of fruits (endozoochory) by birds and mammals or the external movement of seeds with elaiosomes by ants. The vast majority of external transport of seeds with adhesion structures (i.e. epizoochory) has been described in large vertebrates (Bullock *et al.*, 2011). An interesting study described the transport of seeds on the fur of 'transhumant' migrating sheep for several hundred kilometres (Manzano and Malo, 2006). Long-distance dispersal by epizoochory in birds is frequently mentioned as a mechanism with likely important ecological and biogeographical consequences (such as island colonization); however, there is almost no information on this phenomenon which might be largely confined to water birds (Figuerola and Green, 2002; Nogales *et al.*, 2012). Recent evidence suggests that in migrating passerines in Portugal, endozoochory is at least two orders of magnitude more common than epizoochory (Costa *et al.*, in press).

Consequences of Seed Dispersal

Although the advantages of seed dispersal for plant reproductive fitness and vegetation structure have been largely accepted, quantifying such effects has proven methodologically challenging (Wang and Smith, 2002; Levine and Murrell, 2003; García *et al.*, 2005). This is due to (i) the complexity of the process, which involves the simultaneous dispersal of many different seeds by different vectors to different distances and in all directions; (ii) a practical difficulty in measuring seed movement, particularly at longer distances; (iii) the difficulty in correctly monitoring the variability of each step of the process in both space and time; and (iv) problems in tracking the effects of seed dispersal up to the establishment of long-lived adult plants (Herrera, 1998; Levey and Benkman, 1999; Wang and Smith, 2002). Despite such challenges, a growing interest in seed dispersal and its consequences for natural communities has resulted in significant advances in the field towards providing answers to old and new hypotheses, which are constantly being put to the test with rapidly emerging empirical and theoretical evidence.

Seed rain and dispersal effectiveness

The output of seed dispersal sets the spatial framework upon which seeds have to survive, germinate and recruit in order to become established as reproductive adults incorporated into local communities. Therefore, the seed shadow, i.e. the spatial distribution of dispersed seeds around their parent plant, and seed rain, i.e. the sum of all conspecific seed shadows in a certain area, have important consequences for the subsequent processes of plant establishment (Janzen, 1971; Willson, 1993).

Although dispersal is a key parameter in models that seek to understand species distributions (Chisholm and Lichstein, 2009), not many studies have yet linked seed dispersal with its demographic consequences, or provided reliable estimates of seed dispersal effectiveness (Côrtes *et al.*, 2009; Rodríguez-Pérez and Traveset, 2012). Furthermore, studies which have followed the complete sequence of plant regeneration show that focusing on a single stage can lead to misleading conclusions, strongly suggesting that a thorough analysis of seed dispersal effectiveness is vital for solid inferences about the consequences of dispersal (Wright *et al.*, 2000; Rodríguez-Pérez and Traveset, 2007; Côrtes *et al.*, 2009; Figueroa-Esquivel *et al.*, 2009; Calviño-Cancela, 2011).

Disperser effectiveness is the contribution of a disperser to plant fitness (Schupp, 1993), or more practically, the number of plant recruits resulting from the activity of each disperser relative to other dispersers, abiotic disperser or non-dispersed seeds (Calviño-Cancela and Martín-Herrero, 2009). Such a contribution is dependent on a sequence of steps, which can be divided into two main groups: (i) those related to the quantity of seeds dispersed (quantitative component); and (ii) the probability of each dispersed seed to survive, germinate and be recruited as a new adult (qualitative component) (Schupp, 1993; Schupp *et al.*, 2010). Thus, although the initial quantitative component varies greatly according to the number of animal visits, feeding rate and handling technique, the treatment and deposition site also varies greatly between dispersers, which frequently have determinant consequences for

the final pattern of recruitment (Jordano and Schupp, 2000; Calviño-Cancela and Martín-Herrero, 2009). An extreme example of the importance of the quality of seed deposition is the disproportionate arrival of seeds to favoured establishment sites, known as directed dispersal (Howe and Smallwood, 1982; Wenny, 2001). On the other hand, low quality seed dispersal can in fact reduce plant fitness whenever fruits are a limiting factor for recruitment (Jordano and Schupp, 2000). The net result is that different dispersers can have very different dispersal effectiveness based on their quantitative or qualitative effects on germination (Nogales *et al.*, 2005; Padrón *et al.*, 2011) and although merging dispersers into functional groups can be useful as a first approach to their effectiveness (e.g. seed predators, pulp feeders, guppers, etc; Jordano and Schupp, 2000), it seems that often dispersers lay along a continuum from poor to good dispersers (Heleno *et al.*, 2011). Two factors that largely determine the quality of seed dispersal are the deposition site and the effect of seed ingestion (in the case of endozoochory) on seed germination rate, which can be either accelerated or slowed down depending on both the seed and the disperser (Traveset, 1998; Traveset *et al.*, 2001). The germination asynchrony resulting from the heterogeneity of interactions might have an important adaptive value in unpredictable environments, leading to changes in at least some seeds so that they germinate during more favourable periods (Moore, 2001; Mooney *et al.*, 2005).

The advantages of seed dispersal

The advantages of seed dispersal can be divided into three non-exclusive categories of hypotheses: (i) escape from density-dependent mortality in which dispersed seeds have increased fitness by escaping disproportional mortality near the parent plants, due to high predation rate, acquisition of pathogens or conspecific competition (Connell, 1971; Janzen, 1971; Harms *et al.*, 2000); (ii) colonization of newly available sites ensures that the main advantage of dispersal is the chance occupation of favourable sites that are unpre-

dictable in time and space (Holmes and Wilson, 1998); and (iii) directed dispersal where dispersed seeds benefit from non-random deposition in sites appropriate for establishment and growth (Wenny, 2001).

The debate about recruitment probability in relation to distance from the parent plant has been one of the most exciting and controversial debates in plant ecology (Nathan and Casagrandi, 2004). The Janzen–Connell hypothesis (Connell, 1971; Janzen, 1971) proposes that the density of dispersed seeds decreases with increasing distance from the parent plant, but because of a reduced impact of distance- and density-responsive seed and seedling enemies, propagule survival increases, resulting in peak recruitment at some distance from the parent and little recruitment near adult conspecifics. This pattern has received considerable empirical support (Silander, 1978; Wills *et al.*, 1997; Harms *et al.*, 2000; Jansen *et al.*, 2008; Choo *et al.*, 2012), yet it has resisted broad generalization as the effect seems to be largely species specific (Hyatt *et al.*, 2003). Moreover, definitive tests of this model require a demonstration that effects carry over to recruitment of new reproductive adults, however few studies have gone beyond early development stages (Schupp and Jordano, 2011; but see Steinitz *et al.*, 2011).

While the advantages of seed dispersal for plants can be categorized according to the scale on which they operate (e.g. populations, communities, etc.), such divisions are mostly for our convenience, as all these levels continuously and reciprocally affect each other. Consequences on other levels, such as evolutionary (Riera *et al.*, 2002; Chen and Chen, 2011; Schaefer, 2011; Pickup and Barrett, 2012), economic (Fujita and Tuttle, 1991; Hougner *et al.*, 2006; García *et al.*, 2010), or for the dispersers (Chapter 2, this volume) would require a differentiated approach, which is beyond the scope of this chapter. Next, we briefly point out the main consequences of seed dispersal at five levels of biological organization, from genes up to global biogeography.

Genes

Seed and pollen dispersal are the two main processes available for plant gene movement,

and particularly seed dispersal is the only method available for moving genes of self-fertilized flowers and maternally transmitted genes in outcrossing plants. When seed dispersal is low, genetic structure can give rise to 'genetic neighbourhoods' on a relatively small scale (Gibson and Wheelwright, 1995; Nagy and Rice, 1997). However, dispersal by animals can impose distinct spatial signatures in gene flow, resulting from directionality or clustered seed dispersal even at long distances, for example by seed-caching animals or those which use dormitories (García *et al.*, 2007; Pringle *et al.*, 2011).

Therefore, the dispersal pattern of seeds contributes to the genetic structure of populations and the genetic relatedness between seedlings, in turn affecting plant fitness as a result of competition, facilitation, genetic drift and natural selection (Donohue, 2003; Koelewijn, 2004; Crawford and Whitney, 2010; García and Grivet, 2011). Furthermore, at least occasional passage of genes out of a local neighbourhood or between populations is important in maintaining the genetic diversity of the recipient population, which is particularly valuable in a scenario of fragmented populations (Hanski and Gilpin, 1997; Figueroa-Esquivel *et al.*, 2009; Calviño-Cancela *et al.*, 2012).

Because there are so many factors affecting the genetic structure of populations, it remains a challenge to determine the exact importance of seed dispersal to plant population genetic structure, but several studies unequivocally show that such effects exist (Duminil *et al.*, 2007; Wang *et al.*, 2007; Voigt *et al.*, 2009; Zhou and Chen, 2010). Long-distance dispersal, in particular, increases genetic diversity within populations and reduces genetic diversity among populations (Ray and Excoffier, 2010), thus slowing down the rate of population differentiation (Linhart and Grant, 1996).

Populations

Seed dispersal is well documented to influence colonization rate, population spread and persistence and metapopulation dynamics (Levin *et al.*, 2003; García *et al.*, 2005; Mendoza *et al.*, 2009; Schupp *et al.*,

2010). In fact, dispersal is inherent to the very concept of plant metapopulations, broadly defined as spatially disjoint populations linked by dispersal (Hanski and Gilpin, 1997; Cain *et al.*, 2000). In unpredictable and highly disturbed environments, dispersal can allow metapopulation persistence through dispersal from one temporally favourable site to another, even if the growth rate in all local populations is negative (Metz *et al.*, 1983), thus providing a rescue effect for small populations in sink habitats (Brown and Kodricbrown, 1977).

Seed dispersal seems to be particularly important in early successional communities and in the case of expanding populations, such as plant invasions (Hovestadt *et al.*, 2000; Traveset and Richardson, 2006; Iponga *et al.*, 2008). However, all species that cannot be competitive in climax communities are destined to local extinction and are in this sense 'fugitive' species largely dependent on dispersal for long-term survival (Holmes and Wilson, 1998).

Despite its potential demographic importance, intra- and inter-population variation in the assemblages of dispersers has not been well documented (Jordano, 1994; Traveset, 1994; Loiselle and Blake, 1999; Padrón *et al.*, 2011). However, when such studies have been possible, reduced recruitment has been reported as a likely response to lack of appropriate dispersal (Voigt *et al.*, 2009; Rodríguez-Pérez and Traveset, 2010; Traveset *et al.*, 2012).

The search for a relationship between dispersal distances and plant abundance in equilibrium populations has led to ambiguous results (Eriksson and Jakobsson, 1998; Bolker and Pacala, 1999; Thompson *et al.*, 1999), with little evidence of a general pattern (Levine and Murrell, 2003). The causes of this spatial 'uncoupling' are mainly attributed to the spatiotemporal variation in the relative importance of mortality factors (e.g. predation, pathogens, competition) for seeds and seedlings (Houle, 1998). Plant population dynamics in patchy environments depend on patch suitability across all stages (Schupp and Fuentes, 1995; Aguiar and Sala, 1997; Forget, 1997). For example seed-seedling conflicts may exist when a microhabitat offers high

probability of seed survival but low seedling survival or vice versa (Jordano and Herrera, 1995; Rodríguez-Pérez and Traveset, 2010).

Community

Superior competitors and colonizers are thought to be able to coexist because the superior competitor cannot rapidly fill all available niches, allowing some free space for the weaker competitor yet better colonizer species (Horn and MacArthur, 1972; Tilman, 1994; Holmes and Wilson, 1998). Colonization ability is a function of both fecundity and dispersal ability (Holmes and Wilson, 1998; Levine and Murrell, 2003; Murrell and Law, 2003; Muller-Landau *et al.*, 2008). While competition and dispersal/fecundity trade-offs might enable equilibrium coexistence in spatially variable habitats (Yu and Wilson, 2001), clear empirical support for the importance of dispersal in such trade-offs is still scant (Levine and Murrell, 2003). Supporting this idea, Seidler and Plotkin (2006) showed that tree-species spatial distribution patterns in tropical forests are highly correlated with their dispersal mode (Muller-Landau and Hardesty, 2005).

Recent studies suggest that local community diversity is largely limited by the regional species pool (Srivastava, 1999; Turnbull *et al.*, 2000). Although the influence of dispersal on community structure is only beginning to be rigorously examined (particularly in the context of habitat fragmentation, plant invasions and global climate change) (Bacles *et al.*, 2006; Wright *et al.*, 2009; Hampe, 2011; Traveset and Richardson, 2011), its importance seems intuitive as dispersal is known to influence population spread and persistence (Howe and Smallwood, 1982; Howe and Miriti, 2000). However, such variables are very different from most measures of community structure, which include patterns of abundance, distribution and coexistence in climax communities (Levine and Murrell, 2003).

An interesting, yet largely unexplored, question in seed dispersal at the community level is how interactions between seeds and animals other than legitimate seed dispersal, e.g. parasitism, disease, herbivory, plant competition, root symbiosis, etc., affect plant

recruitment patterns. Evidence suggests that many such processes can greatly influence the outcome of seed dispersal leading to highly complex and unexpected outcomes. Some of these interferences to seed dispersal occur before seeds are even removed from the mother plant, such as fruit and seed predation and pathogen attack (Beckman and Muller-Landau, 2011), while others occur after seeds are dispersed, such as secondary dispersal (Nogales *et al.*, 2007), postdispersal seed predation (Orrock *et al.*, 2006) or indirect interactions such as scatter hoarder predation (Steele *et al.*, 2011).

Ecosystem

The final destination of a seed depends not only on seed morphology and the dispersal vectors, but also on the interaction between these and habitat structure or topography, which traps or sorts propagules at different scales – a less appreciated and more difficult to predict determinant of dispersal kernels (Levine and Murrell, 2003; García *et al.*, 2011). Because plants, particularly large trees, can physically shape landscape characteristics and the distribution of those plants simultaneously affects and is affected by seed deposition patterns, feedback loops between species composition, seed dispersal and habitat structure are to be expected (Purves *et al.*, 2007). For example by attracting seed dispersers, isolated plants can act as dispersal foci for many forest plants, as seeds accumulate under their canopies after visits by frugivores (Zahawi and Augspurger, 2006; Kelm *et al.*, 2008; Herrera and García, 2009; Morales *et al.*, 2012).

The signature of animal seed dispersal on habitat features has been shown in several systems, including bird-mediated dispersal of invasive trees driving savanna nucleation processes (Milton *et al.*, 2007), bat dispersal-assisted tropical forest recovery (Kelm *et al.*, 2008), elephant-driven spatial distribution of trees (Campos-Arceiz and Blake, 2011), and ant-selected community composition (Christian, 2001). Even on a geological time-frame, ecosystems depend on the ability of plants to adapt to changing climate, which is largely dependent on their

long-distance dispersal potential (Clark *et al.*, 1998; Higgins *et al.*, 2003a; Hampe, 2011).

Biogeography

The way that seeds are moved over long distances can have consequences that go beyond the landscape level and influence the global distribution of plants, i.e. biogeography. At this level, seed dispersal is particularly important in determining plant 'migration' rates, for example tracking favourable climatic conditions such as after glaciations (Clark *et al.*, 2003; Powell and Zimmermann, 2004; Corlett, 2009), or as a consequence of recent anthropogenic climate change (Pitelka *et al.*, 1997; Higgins and Richardson, 1999). Other global processes that are largely influenced by the facility of seeds to travel over long distances are the spread of invasive species (Bartuszevige and Gorchoy, 2006; Brochet *et al.*, 2009) and the colonization of oceanic islands by plants (Nogales *et al.*, 2012; Vargas *et al.*, 2012). In the latter case, seed dispersal is determinant as all native vegetation of oceanic islands, i.e. those that emerged from the sea floor and were never connected to a continent, had to initially cross the sea barrier, usually in the form of seeds dispersed by sea currents, wind or animals (see section entitled 'The Determinants of Seed Dispersal', p. 63, this chapter).

Seed Dispersal and Conservation Implications

Seed dispersal is universally considered important for biodiversity conservation. Seed dispersal by animals, in particular, is considered a pivotal ecosystem function that drives plant-community dynamics in natural habitats and vegetation recovery in human-altered landscapes. Nevertheless, there is still a lack of suitable ecological knowledge to develop basic conservation and management guidelines for this ecosystem service (Gosper *et al.*, 2005; García *et al.*, 2010).

The structure of the landscape has strong effects on the distances travelled by

seeds, regardless of the dispersal mode. Hence, any type of disturbance such as habitat fragmentation or modification by an invasive plant species is likely to change the patterns of seed movement and recruitment, as well as the genetic structure of plant populations. Wind-dispersed seeds travel much further in open landscapes than in dense forest, due to differences in the shape of the wind profile. By contrast, plants depending on animals for seed movement are susceptible to dispersal failure when their seed vectors become rare or extinct (Traveset and Richardson, 2006).

Disruption of seed dispersal mutualistic interactions can have serious consequences for the population maintenance of the organisms involved, but especially for the plant. An increasing number of studies are showing how the populations of seed dispersers are being decimated, both in the tropics and in the temperate zones, and how this translates into a lower dispersal success of the plants depending upon their services (Wotton and Kelly, 2011; Rodríguez-Pérez and Traveset, 2012; Traveset *et al.*, 2012; Young *et al.*, 2012). In tropical areas in particular, the widespread decline of dispersers by overhunting, selective logging and fragmentation is expected to have long-term negative consequences for the maintenance of tree species diversity (Wright *et al.*, 2000; Markl *et al.*, 2012). A recent meta-analysis indicates that disrupted plant–frugivore interactions could actually trigger a homogenization of seed traits in tree communities of disturbed tropical forests, as hunting and logging show a differential effect on the dispersal of large versus small-seeded tree species (Markl *et al.*, 2012).

Species response to habitat loss and fragmentation

The response of plant species with different dispersal modes to habitat loss is highly variable. A study by Montoya *et al.* (2008) examining the responses of 34 tree species found that animal-dispersed species were less vulnerable to forest loss than those

dispersed by other vectors, thus suggesting that plant–animal interactions can help to prevent the collapse of forest communities after habitat degradation.

One question which has only recently started to be addressed is whether a diverse assemblage of dispersers is important to sustain a high quality of seed dispersal services in a community, as reported for the pollination service (Biesmeijer *et al.*, 2006; Fontaine *et al.*, 2006). The first results suggest that despite frugivore abundance being a good surrogate of landscape-scale seed dispersal and an indicator of patch quality for the dispersal function (García *et al.*, 2010), the identity of dispersers might also play an important role (García and Martínez, 2012). More data from different systems are needed to assess how generalized these results are. In the agricultural matrix in Costa Rica, for example, bird abundance rather than diversity best predicted the richness of bird-dispersed seeds (Pejchar *et al.*, 2008). In Central Europe, the ecosystem function is apparently unaltered in areas of high human land use mainly because birds have increased their foraging flying distances to locate fruits (Breitbach *et al.*, 2010). Other systems have been shown to be more vulnerable to forest degradation, such as the effective dispersal of seeds from many bushes and trees in a vast number of tropical freshwater systems (Horn *et al.*, 2011).

The emergence of novel communities

Throughout the world, alien invasive species rank among the most serious threats to native biodiversity and are considered a major factor of global change (Millennium Ecosystem Assessment, 2005). A recent review on the dispersal mode of 622 alien plant species has shown that birds are the most important agent of dispersal for invasive alien trees (c.43%) and shrubs (c.61%), with wind being the second most important vector (Richardson and Rejmánek, 2011). Furthermore, increasing evidence is showing that propagule pressure, determined by seed dispersal, is important in invasive plant

establishment and spread (Milton *et al.*, 2007; Simberloff, 2009). Nowadays, we also know that seed dispersal has direct consequences on vegetation structure and may be particularly decisive in a scenario of plant invasions, in which frugivores include the fruit of invasive plants into their diets and consequently facilitate their establishment and spread (Nathan and Muller-Landau, 2000). An illustrative example of how a plant–frugivore interaction may promote an invasion that changes the entire community structure was provided by Milton *et al.* (2007). These authors reported that birds facilitate the invasion of arid savannas in South Africa, where alien fleshy-fruited plants infiltrate prevailing seed dispersal networks. Once infiltrated, the natural dispersal network is disrupted because some invasive plants transform the savannas by overtopping and suppressing native trees that act as crucial perching sites and foci for directed dispersal (Iponga *et al.*, 2008).

Although the role of seed dispersal processes in biological invasions has still received relatively little attention (see a review in Westcott and Fletcher, 2011), an increasing number of studies report how invasive species are integrated into natural dispersal communities (Milton *et al.*, 2007; Padrón *et al.*, 2011; Heleno *et al.*, 2013a,b) as well as how intruders affect native dispersal interactions (reviewed in Traveset and Richardson, 2011; López-Bao and González-Varo, 2011; Rodríguez-Cabal *et al.*, 2012). Clear examples of dispersal disruptions have been documented mainly in oceanic archipelagos such as Hawaii (Chimera and Drake, 2010) and the Canary Islands (Nogales *et al.*, 2005; López-Darias and Nogales, 2008). Competition between natives and invaders for mutualistic partners is often being reported, although it is not yet clear to what extent such competition affects native populations rather than just facilitating the spread of invaders. However, it seems likely that plant–seed disperser (as well as pollinator) interaction webs will be irreversibly adjusted in these novel communities in response to the spread of invaders (Ghazoul, 2005). Further work is needed across different species and ecosystems to better understand the overall cost of native

mutualistic disruptions, but the evidence so far indicates that this can be quite high (Traveset *et al.*, 2012).

Long-distance dispersal of seeds has caused surprisingly fast invasion rates in many species (Nathan, 2006). It is somehow paradoxical that long-distance dispersal, which is disproportionately important for plant biodiversity and conservation, is, at another level, the root of one of the great threats to biodiversity in the form of human-increased long dispersal of alien invasive species (Trakhtenbrot *et al.*, 2005).

Another paradox can be found in those cases in which native plants currently rely exclusively on alien seed dispersers. This has been reported, for instance, for most common understorey native plants in Hawaiian rainforests, dispersed by alien birds (Foster and Robinson, 2007). Another case can be found in the Balearic Islands where alien pine martens are the main dispersers of plants that used to be dispersed by currently extinct native lizards (Traveset *et al.*, 2012). More research in other systems is necessary to assess how common such replacements are and to what extent the ecosystem function is maintained with these new dispersers. Fortunately, most plant–disperser interactions are generalized and a tight specialization of dispersers does not seem to be required in order to achieve highly effective dispersal (Calviño-Cancela, 2002, 2004). However, seed dispersal by simplified fauna composed of abundant and generalist species is likely to accelerate species shuffling according to their abundance and thus accelerate the homogenization of biota, even if resulting in highly connected and highly nested (i.e. robust) communities (McKinney and Lockwood, 1999; Heleno *et al.*, 2012). If both mutualists are alien, and facilitating each other's spread, as is often the case, then we are faced with an 'invasional meltdown' (Simberloff and Holle, 1999; Simberloff, 2006).

Effect of climate change

Climate change is another major driver of global change that presents a potentially

severe threat to biodiversity. Climatic models show that species will be required to disperse rapidly through fragmented landscapes, across both latitudinal and altitudinal gradients in order to keep pace with the changing climate (Pearson and Dawson, 2005). Hampe (2011) reviews the empirical evidence for the role of long-distance seed dispersal in past and ongoing expansions, and examines how some major ecological determinants of seed dispersal and colonization processes might be altered by a rapidly changing climate. Relating dispersal processes and pathways with the establishment of pioneer populations ahead of the continuous species range remains a real challenge. An in-depth treatment of the relationship between seed dispersal and climate change is given in Chapter 9.

Restoration of seed dispersal processes

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 between species (Memmott *et al.*, 2007; Heleno *et al.*, 2010; Kaiser-Bunbury *et al.*, 2010; Tylianakis *et al.*, 2010). The restoration of the seed dispersal function is crucial for the long-term stability of restored communities (Handel, 1997). Seed dispersal to a great extent determines vegetation structure (Wang and Smith, 2002), such that the incomplete restoration of such an important ecosystem service may actually result in a community failing to be self-sustaining (Kremen and Hall, 2005). Moreover, even if restoration results in the recovery of species diversity this does not guarantee that the processes in which those species are involved, such as seed dispersal, are re-established (Palmer *et al.*, 1997; Forup *et al.*, 2007).

The preservation of the seed dispersal process and its mobile agents should be considered a tool for passive and hence low-cost ecological restoration (Howe and Miriti, 2004). A land-management approach trying to maintain and increase the presence

of scattered remnant trees over a deforested matrix might accelerate secondary succession through a process of facilitation mediated by seed dispersers (Valladares and Gianoli, 2007; Herrera and García, 2009). A recent study carried out in southern Spain has shown that the seed rain produced by frugivorous birds on a tree plantation is strongly determined by the nature of the surrounding vegetation (Zamora *et al.*, 2010). Recent simulation studies have also found that fruit removal rates and mean dispersal distances are strongly affected by fruiting plant neighbourhoods (Morales *et al.*, 2012). Plants in denser neighbourhoods had greater fruit removal and shorter mean dispersal distances than more isolated plants. The interplay between frugivore behavioural decisions and the spatial distribution of plants could thus have important consequences for plant spatial dynamics and should be taken into account in any restoration programme.

Birds have often been documented as aiding alien plant spread (Bartuszevige and Gorchov, 2006; Williams, 2006; Gosper and Vivian-Smith, 2009). Whenever native and exotic plants do not share the same physical space or the same dispersers, natural or artificial bird perching structures can conceivably be used to direct the dispersal of exotic seeds to unsuitable or easily controlled areas (sink habitats), or to direct the dispersal of native seeds to suitable recruitment sites. Several studies have conducted perch manipulations in the field in order to direct seed dispersal (e.g. Holl *et al.*, 2000; Robinson and Handel, 2000), usually with a clear increase in seed deposition under perches (Wenny, 2001; Shiels and Walker, 2003). Even if the effectiveness of such methods remains a matter of debate (Holl *et al.*, 2000; Robinson and Handel, 2000; Shiels and Walker, 2003), it stands as a practical example of conservation measures that can be greatly enhanced by an in-depth knowledge of seed dispersal systems. Several other more general guidelines based on seed dispersal are frequently implemented by practitioners in conservation projects such as initiating the control

of weeds starting from elevated areas and working downhill (as most seeds will be dispersed in this direction by wind and gravity), or trying to tackle plant invasions before the fruiting season.

Ecological networks can provide a holistic approach to ecosystem management, with benefits for both restoration science and restoration practice (Heleno *et al.*, 2010). In a scenario of ecological restoration, seed dispersal networks can be useful in both the planning stage and the monitoring of restoration effectiveness as they provide a valuable tool to look beyond species composition and into ecosystem functioning. For example, they can be important to predict the potential consequences (positive and negative, direct and indirect) of species introductions or species eradication programmes (Memmott, 2009; Padrón *et al.*, 2009; Hansen *et al.*, 2010). Such an exercise can be useful to identify keystone species, or in the context of seed dispersal, keystone mutualists, which should then be the focus of conservation, management or restoration efforts (Kaiser-Bunbury *et al.*, 2010).

Conservation and restoration priorities are inherently idiosyncratic to each area and it may not always be possible or important to address seed dispersal when restoring a habitat. In the medium to long term, restoration has to tackle seed dispersal interactions but also pollinator interactions to avoid genetic deterioration of the plant community. Small populations of restored plant species will maintain relatively little genetic diversity, which reduces the chance of successful adaptation to small- or large-scale alterations such as climate change. Hence, in a second phase, large-scale, long-term restoration needs to be carried out to account for seed dispersal interactions to eventually result in reproductively self-sustaining communities (Kaiser-Bunbury *et al.*, 2010). In order to predict which ecological interactions are at risk from loss of critical species, empirical comparisons of the population-level impacts of mutualist animals are also necessary (Brodie *et al.*, 2009).

Conclusions and Future Avenues of Research

The study of the dispersal of plants has rapidly advanced in the last two decades, as essential elements of the evolutionary and ecological causes and consequences of dispersal have been examined. Specifically in the last decade, there has been an increasing effort to link the process of seed dispersal and its demographic and genetic consequences. This has been mainly due to the development of several technological tools which allow following seed fate via radio-tracking (Pons and Pausas, 2007), rare isotope enrichment (Morales *et al.*, 2012) or fluorescent markers (Levey and Sargent, 2000), following the movements of dispersers with satellite tracking of long-range seed dispersers such as seabirds, the development of increasingly robust mathematical modelling (Levey *et al.*, 2005), and particularly with the advent of widely available and cost-effective genetic markers (Terakawa *et al.*, 2009; Choo *et al.*, 2012). For example, it is now possible to distinguish between maternally and paternally inherited genes by comparing DNA from the nucleus with that from organelles (chloroplasts and mitochondria) that are inherited from the mother plant (Ouborg *et al.*, 1999). Furthermore, the analysis of several microsatellite loci of the seed endocarp allows matching each seed to its individual mother plant, which in turn permits the study of long-distance dispersal (Godoy and Jordano, 2001; Ziegenhagen *et al.*, 2003; Grivet *et al.*, 2005; Jordano *et al.*, 2007). Such techniques, for instance, allow estimating seed dispersal kernels, characterizing animal foraging behaviour, and understanding the colonization history of oceanic islands by plants (e.g. Rumeu *et al.*, 2011; Vargas *et al.*, 2012). The possibility to identify the disperser species based on surface DNA from droppings and pellets collected in the field has also only come about with molecular tools (Marrero *et al.*, 2009). Much has been advanced towards the integration of multiscales of dispersal (García, 2002), and in following the seed dispersal signature up to the establishment of adult

trees (Calviño-Cancela and Martín-Herrero, 2009). Quantifying seed dispersal patterns at increasingly large scales is a particular challenge due to the uncertain consequences of rare events (Higgins *et al.*, 2003b; Nogales *et al.*, 2012); despite different types of seed traps proving to be highly useful in the study of short-distance dispersal, they are impractical for detecting rare long-distance dispersal events (Greene and Calogeropoulos, 2002). Another important information gap is the lack of long-term studies, which are crucial if we are to link seed dispersal and the distribution of adult trees in natural habitats. A short-cut to address this issue might be to start with the distribution of adult trees and try to predict previous dispersal based on population age structure using dendrochronology and kinship analysis via molecular methods.

It is now widely accepted that animal seed dispersal represents a key process in the functioning of many different ecosystems, from deserts to rainforests, and for the maintenance of their biodiversity (Forget *et al.*, 2011). We also know that this mutualistic interaction is seriously threatened by human activities, which promote fast changes in ecological conditions. New conceptual frameworks such as movement ecology, complex networks of interactions among species (see Box 3.2, this chapter) and their associated ecological functions and services, and landscape-level analyses combined with models of range shifts due to climate change are likely to provide important advances in this field (Jordano *et al.*, 2011). The integration of different disciplines related to seed dispersal that involve different methodologies (including ecophysiology, landscape ecology, population genetics, biogeography, conservation biology, evolutionary ecology and phylogenetics, and climate change biology) is increasingly essential to build mechanistic models and frame robust predictions about the consequences of the loss of plant–frugivore interactions for natural and human-modified habitats. This, in turn, will permit foreseeing critical conservation risks, developing early-warning signals of seed dispersal disruptions, and designing better management plans for

Box 3.2. Seed dispersal networks

Species do not exist in isolation, and therefore the interactions they establish with one another play a determinant role in defining the community structure, the functions performed by ecosystems and the services they deliver to humans (Duffy *et al.*, 2007; Tylianakis *et al.*, 2010). Seed dispersal by animals, in particular, is one such function that greatly illustrates the importance of studying ecological interactions at a community level. Such interactions have been frequently depicted in the form of food webs or more generally as interaction networks composed of nodes (i.e. plants and animals), and links (i.e. dispersal events). The consolidation of this network approach has allowed scientists to simultaneously focus on the effects of conservation efforts on focal species and on the overall community, and contributed to improving the focus of conservation efforts for a more integrated viewpoint (Millennium Ecosystem Assessment, 2005). Seed dispersal is inherently a complex process at many levels. The use of a network approach offers a theoretical framework to look for patterns and general rules without losing information due to clustering species into functional groups.

Although first networks represented antagonistic interactions (who eats whom), rapidly the approach has been translated into mutualistic interactions, stemming from the growing perception that facilitation, like competition, is an important process shaping natural communities (Bruno *et al.*, 2003). Within this context, pollination has received the most attention followed by seed dispersal and more recently by root symbionts (Memmott, 1999; Bascompte and Jordano, 2007; Montesinos-Navarro *et al.*, 2012).

Although in his seminal book, Ridley (1930) compiled information on the dispersal vectors of a large number of plants, only in the 1970s did ecologists begin to empirically document all dispersal events within a single community (e.g. Snow and Snow, 1971; Herrera, 1984). The work by Jordano (1987) formally applied the network theory to the study of seed dispersal, and more recently others have followed (e.g. Donatti *et al.*, 2011; Mello *et al.*, 2011b; Heleno *et al.*, 2013a,b).

Seed dispersal networks can be especially useful for understanding the process of plant invasions, particularly those with fleshy fruits, and there has been an all-out effort to document the dispersers of invasive plants and the plants dispersed by invasive animals (e.g. Milton *et al.*, 2007; Kelly *et al.*, 2010; Linnebjerg *et al.*, 2010; Padrón *et al.*, 2011; Heleno *et al.*, 2013b). However, rigorous information on entire species assemblages of plants, seed dispersers and their interactions is still rarely available (Buckley *et al.*, 2006), which hinders informed decisions in conservation planning (Gosper *et al.*, 2005).

Networks allow us to escape descriptive studies and look for patterns across different communities by means of standard network parameters, and to link those patterns to community stability and functioning (Bascompte and Jordano, 2007), for example between islands and continents (Box 3.1, this chapter).

Although the application of network theory to seed dispersal is still in its youth, some common patterns have been identified such as: (i) a great heterogeneity in the strength of interactions among species; (ii) rarity of strong inter-specific co-evolution between plants and dispersers (Jordano, 1987); and (iii) a high level of asymmetry in the interactions, such that specialist plants tend to depend on generalist dispersers while specialist dispersers depend on generalist plants (Bascompte *et al.*, 2003). Such a characteristic results from a nested pattern between plants and animals, which has been shown to protect communities from cascading extinctions (Bascompte and Jordano, 2007). Furthermore, recent work revealed seed dispersal interactions are arranged in a modular pattern, i.e. with some clusters of species interacting more with each other than with species outside that cluster–module (Donatti *et al.*, 2011). Such a pattern, emerging through a combination of phylogenetic history and trait convergence (Donatti *et al.*, 2011) suggests that despite being a less specialized interaction than pollination (Howe and Smallwood, 1982), species within different modules may follow different co-evolutionary pathways driving adaptations among plants and their dispersers (Mello *et al.*, 2011b).

Regardless of the proclaimed potential of seed dispersal networks for the advance of ecological theory and practice, broad generalizations and application of this approach are still meagre (Carlo and Yang, 2011). We briefly consider four challenges that seed dispersal networks have to overcome in order to meet their full potential.

Continued

Box 3.2. Continued.

More precise networks – Seed dispersal is a multistage process, where each part contributes to the overall outcome (Fig. 3.4). Although the emergence of quantitative networks, which incorporate measures of interaction strength, has been an important advance from qualitative networks, a most necessary step is to include more precise assessments of dispersal effectiveness in seed dispersal networks. Despite effectiveness being the best parameter to quantify interaction strength, it has seldom been used in a network context (Carlo and Yang, 2011). Most often, interaction frequency is used instead as a surrogate of dispersal effectiveness (Vázquez *et al.*, 2005), which ignores the quality of seed dispersal, focusing on its quantity (Schupp *et al.*, 2010). Conclusions based on quantitative proxies might then be misleading (Calviño-Cancela and Martín-Herrero, 2009) and we need to try to incorporate dispersal effectiveness into seed dispersal networks in order to validate how network properties predict ecological outcomes (Tylianakis *et al.*, 2010; Carlo and Yang, 2011).

Bigger networks – Networks are assembled under multiple decisions taken by researchers either for logistical reasons or following their own ‘comfort zones’ (Memmott *et al.*, 2007), which might be taxonomic groups or habitats. Even if seed dispersal does not stop at habitat interfaces, most seed dispersal networks are confined to one functional group of dispersers, frequently birds (Mello *et al.*, 2011a), and to physical or perceived borders in the habitat. In addition, seed dispersal by animals is only one of many interactions that both organisms establish in nature. Seed dispersal networks can thus be included in a wider context of other interactions, in effect a network of networks (Pocock *et al.*, 2012), as these simultaneous interactions can greatly affect the outcome of seed dispersal (e.g. Wright *et al.*, 2000; Steele *et al.*, 2011).

Node characterization – The soundness of the insights gained from analysing seed dispersal networks is dependent on the quality of data and the correct interpretation of results, rather than on sophisticated analytical methods. Thus, while for network analysis all nodes within a level are considered equivalent, all species are distinct in many ways (e.g. behaviour, abundance, conservation value, etc.) which constitutes important information for interpreting the context-specific outputs (Carlo and Yang, 2011).

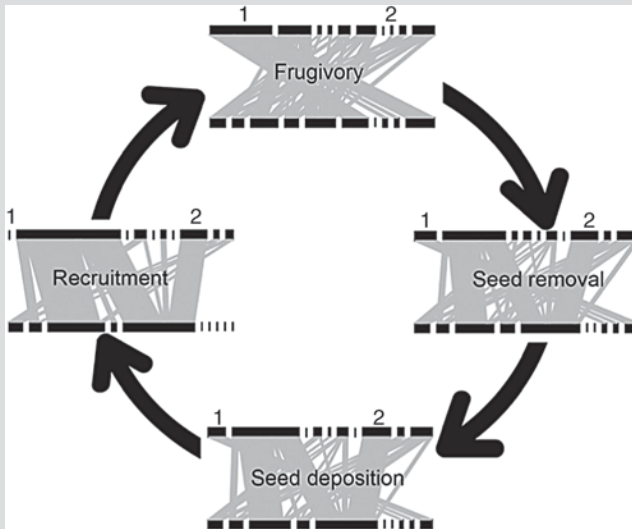


Fig. 3.4. Each network represents successive stages in the whole process of seed dispersal: frugivory, seed removal, frugivore movement and seed recruitment. Although the same species are represented in each network: dispersers on the top row and plants on the bottom row, their relative contribution is largely dependent upon the information used to quantify the interaction strength in each network. (From Carlo and Yang, 2011.)

Continued

Box 3.2. Continued.

For example, one should not dismiss concepts of species conservation value when translating network results for a conservation scenario (Heleno *et al.*, 2012). For instance, while high specialization can contribute to increasing the vulnerability to disruption (Aizen *et al.*, 2012), to protect vulnerable specialist species might be the appropriate conservation target as high network robustness can be a consequence of the previous extinction of specialists or the accumulation of generalist species (Menke *et al.*, 2012), both of which can represent environmental degradation and not a direct indicator of conservation value (Heleno *et al.*, 2012).

Better experimental design – The progress made in the development of mathematical tools to describe interaction networks contrasts with the scarcity of empirical data to feed them, which is vital to validate network model predictions (Carlo and Yang, 2011; Heleno *et al.*, 2013a). A major difficulty has been the *a posteriori* comparison of networks assembled by different researchers for different ends and which vary greatly in the sampling protocols, sampling effort and taxonomical resolution. In order to increase the statistical power and the likelihood of detecting emerging patterns, it is important to plan robust experimental designs or wait for enough high-quality studies to become available for meaningful meta-analysis.

In conclusion, network theory provides ecologists with an important tool to examine the intricate web of interactions between plants and their dispersers; however, whether networks become fully informative will depend on our ability to put theory to the test with more and better datasets and appropriate experimental designs explicitly set to test network-driven predictions.

efficient restoration of ecological functions (Forget *et al.*, 2011; Jordano *et al.*, 2011). We also need to consider that the effects of different types of disturbance (e.g. frugivore hunting, fragmentation, invasions, climate change, etc.) are not only ecological (e.g. truncating dispersal kernels, changing density-dependent plant mortality at different stages of the life cycle), but also evolutionary. Direct anthropogenic impacts on the community of dispersers may translate into rapid evolutionary shifts in seed and fruit traits (Wotton and Kelly, 2011; Markl *et al.*, 2012).

The field of dispersal ecology also needs to be more integrated with that of invasion ecology (and vice versa), as Westcott and Fletcher (2011) have pointed out. Invasions represent ‘natural’ experiments that allow testing models related to dispersal processes and their influence on population and community structure. Moreover, they can contribute to the understanding of the evolution of dispersal-relevant traits such as seed size (Muller-Landau, 2010). A detailed and integrated understanding of dispersal processes is also important to effectively manage biological invasions (Traveset and Richardson, 2011).

When considering the conservation and restoration of ecosystem functions, such as that provided by seed dispersers, it is increasingly

recognized that network theory is a particularly valuable tool in providing a structural and functional approach to frame the whole community and the full variety of inter-specific interactions that hold communities together (Carlo and Yang, 2011; Cruz *et al.*, in press). Such an approach may be particularly useful on islands due to the simplicity of ecosystems (Kaiser-Bunbury *et al.*, 2010), although it should also be valid for continental habitats. Insights gained through an increasing number of mutualistic networks encompass similar interaction patterns at the guild or ecosystem level between communities (Bascompte *et al.*, 2006; Olesen *et al.*, 2007). One major challenge, however, is to adequately capture and describe the spatial and temporal dynamics of mutualistic networks (Bascompte and Jordano, 2007; Olesen *et al.*, 2008; Tylianakis, 2008). Such network analyses appear to be promising as well, to detect geographical patterns, colonization and extinction dynamics of native species, and appear particularly useful to study the functioning of the novel ecosystems emerging due to the movement of species across the planet.

In short, dispersal ecology is a rapidly developing field that offers a wealth of investigative opportunity at many different levels, ranging from good natural history to sophisticated modelling and conceptual synthesis.

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