

Effect of dispersal ability on plants' range shifts caused by contemporary climate change

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Abstract

Because of the climate warming during the 20th century, species shift their range to track their preferred climates (Parmesan & Yohe, 2003). However, while some species already show considerable range shifts, many species have not (yet) shifted their range (Lenoir et al., 2008). There is growing interest into whether certain plant traits, such as dispersal ability, could predict which species are able to move their range (Angert et al., 2011). Next to research directly examining the effect of dispersal traits on range shifts, research examining the effect of traits on plants' range size and range filling (the extent to which a species inhabits its potential area) can give information about what traits affect range shift ability, since these traits could also help a species to successfully establish in a new habitat (Estrada et al., 2016). However, since the actual seed dispersal distance of many species is not known, studies often use simple plant traits to estimate dispersal capacity (Vittoz & Engler, 2007). By looking at studies examining the effect of dispersal traits on range shifts, range size and range filling, this paper examines which traits are used to determine dispersal capacity, and whether current evidence suggests that these traits indeed influence range shift ability. Most studies reviewed found that dispersal modes which reach longer distances, such as dispersal by wind or animals, increase range shift ability in plants. However, evidence for an effect of seed size or seed mass on range shift ability is mixed. This paper gives insight in which dispersal traits influence range shifts, and gives direction as to which dispersal traits need more research.

Introduction

The climate is warming more rapidly in the 20th century than ever before in recent history, with temperatures on average rising with about 0,6 °C (Jones et al., 2001). This trend is expected to proceed in the current century, with temperatures in Europe rising between 0,1 and 0,4 °C per decade (IPCC, 2001). Plants can react to this warming in different ways. More and more evidence suggests that plants use phenotypic changes to keep up with climate change, such as earlier blooming. However, because of the rapid rate of climate change, the capacity of plants to keep up with climate change by phenotypic plasticity is likely to be overpassed (Jump & Peñuelas, 2005). Similarly, plants ability to adapt to climate change evolutionarily is likely not large enough to adapt to their new environment (Jump & Peñuelas, 2005). As a consequence, plants need to move their range to areas where they can still tolerate the environmental conditions. Evidence for these range shifts is mostly found in the arctic (Serreze et al., 2000) and in mountains, where plants move upwards (Bertrand et al., 2011; Lenoir et al., 2008). Although there is strong evidence for range shifts (Parmesan & Yohe, 2003), species differ strongly in the strength and even direction of range shifts. For example, even though Lenoir et al. found an average upward range shift of 29 meters per decade, only two third of the species shifted their range upwards, whereas one third of the species shifted their range downwards (Lenoir et al., 2008). Consequently, some species may be able to track the changing climate, while species that cannot shift their range quickly enough, may face a reduced population size or become extinct.

One of the reasons that species may not keep up with climate change, is because of dispersal limitations (Bertrand et al., 2011). Since plants can only move during seed stage, seed distribution and survival determines the extent to which plant populations can move (Corlett & Westcott, 2013). Some traits of seeds can influence how far seeds disperse, such as the method of dispersal (Angert et al., 2011; Felde et al., 2012), seed size (Wolf et al., 2016; Zhu et al., 2012) and ability to self-fertilize (Estrada et al., 2015). Recently, dispersal characteristics are used to see whether plants with certain characteristics are more likely to shift their range than others (see table 1 in the annex for references).

However, since there are only few studies measuring the effect of dispersal traits on range shifts directly, some proxies for range shifts are also used, such as range size and range filling (Estrada et al., 2016). A plants' range size may give an indication of its range shift ability, since the plant was presumably able to expand their range in the past (Estrada et al., 2016). In Europe, for instance, current plant distributions may be influenced by the last glacial period. Plants that have expanded their range since then, may have traits that facilitate this movement (Estrada et al., 2015). Similarly, range filling determines the potential range that a plant can occupy, and compares this to the proportion of the potential range that it actually occupies. If a plant is only present in a small part of its potential range, it may be due to dispersal limitations, or sensitivity to biotic interactions that limit its range. If these factors influence its range now, it may influence its range shift ability in the future as well (Estrada et al., 2016).

Still, studies use very different measurements of dispersal, making it difficult to determine which factors are more important (Estrada et al., 2015). More knowledge about which dispersal traits influence range shifts can help determine which species are in danger of becoming extinct because of climate change, which can inform conservation programs about which species need to be protected (Angert et al., 2011). This paper discusses the different dispersal traits and the effect they might have on plant dispersal. Afterwards, several papers will be reviewed to see whether these traits actually influence range shifts. This paper will answer the question;

- How do dispersal traits affect the range shifts of plants in response to climate change?

With the subquestions;

- What plant traits are used to determine dispersal potential?
- What is the evidence of the effect of dispersal traits on range shifts?
- Can information from other metrics, that have been determined already over longer periods, such as range size, range filling and invasion potential give information about the effect of dispersal traits on future range shifts?

What plant traits are used to determine dispersal potential?

Dispersal ability is often mentioned as an important reason why plants cannot shift their range following climate change. Plants that have limited dispersal ability, may have more difficulty colonizing new areas and supplying enough individuals to establish a viable population (Lester et al., 2007), and therefore have a limited range shift when new areas become suitable because of climate change. However, there is currently little evidence for this hypothesis. One of the reasons for this could be that data about dispersal distances is not always known, and therefore difficult to incorporate in a study (Vittoz & Engler, 2007). There are no dispersal distances available for entire regional flora, and often databases are (partly) based on anecdotal observations. Therefore, it is necessary to establish estimates of dispersal distances for plants based on plant traits which are more easily available (Vittoz & Engler, 2007). However, studies use a wide variety of traits to determine dispersal potential, and these are not always good indications of real dispersal potential (Estrada et al., 2015). Table 1 in the annex shows the reviewed literature on the effect of dispersal traits on range shifts, range filling and range size. Here, the plant traits which are most often used are listed, and why they would influence dispersal and range shifts is reviewed.

Seed dispersal mechanism

One of the most often tested hypothesis is whether species with a certain dispersal mode shift their range faster than others. (Angert et al., 2011; Felde et al., 2012; Holzinger et al., 2007). Usually in literature, six main types of dispersal modes are recognized; dispersal by wind (anemochory), ingestion by vertebrates (endozoochory), ants (myrmecochory), explosively ejecting the seeds (ballistichory), the attachment of seeds to fur or feathers (epizoochory) and unassisted dispersal (Hughes et al., 1994). Within these categories, more specific dispersal modes can be identified, and there are large differences in the effectiveness of each dispersal mechanism. Vittoz & Engler (2007) reviewed literature on dispersal distances of different dispersal modes, and gave the upper limits of the distance that 50% and 99% of the seeds of each mechanism disperse. Except for dispersal by humans, transport by animals (endo- and epizoochory) had the largest average dispersal (400 m), while the smallest average distance was only 0,1 m and reached by blastochory (dispersal where the parental plant grows as far as possible on the ground to deposit the seeds), boleochory (dispersal where seeds are released when the fruit is shaken by the wind or animals), and ombrochory (dispersal where seeds are dispersed by the rain drops hitting the fruits) (Vittoz & Engler, 2007). Similarly, Thomson et al. (2005) found much larger dispersal distances of dispersal by animals (both by ingestion and attachment to fur) than dispersal by wind, even though wind dispersal is often considered as a good mechanism for long distances. However, differences between species with the same dispersal mechanism is often considerable (Thomson et al., 2005; Vittoz & Engler, 2007).

Within seed dispersal mechanisms, seeds have different attributes that help advance their dispersal, such as a pappus and wings for wind dispersal, or hooks for attachment to fur or feathers (Welling et al., 2005). Within wind dispersal, appendages are regularly found, since they reduce the falling speed of the seed and as a consequence increase the dispersal distance (Parolo & Rossi, 2008). Since the dispersal mechanism of species partly depends on the abiotic factors of the environment, some areas have a strong bias towards certain dispersal modes (Hughes et al., 1994). For example, wind dispersal may be more common in early succesional habitats, while dispersal by animals becomes more common in later stages of succession (Hughes et al., 1994).

Seed size

Seed size may influence dispersal distance and success in various ways. Large seeds have several advantages. Large seeds contain more nutrients, and therefore large seeds produce larger seedlings which survive more easily during the first stage of life (Moles et al., 2004). These seedlings are more tolerant towards stress factors, such as shade, drought and shortage of nutrients (Moles et al., 2004). Moreover, seedlings from large seeds can survive more easily when in areas with strongly closed vegetation (Welling et al., 2005). However, species with small seeds produce more seeds; if the seeds mass increases 10-fold, the number of seeds that the plants produce per unit of canopy decreases 10-fold (Moles et al., 2004). Because of the larger number of seeds, the chance that one of these reaches a new suitable area increases (Estrada et al., 2015). Moreover, small seeds may survive longer periods in the ground, and as a consequence the seeds are more tolerant to bad environmental conditions (Hamilton et al., 2005). Because of this, many studies use seed size as a factor (table 1 in annex).

Since life-history traits are generally inter-related, seed mass has a positive correlation with several other traits (Hamilton et al., 2005). For instance, seed mass can be linked to dispersal mode; light seeds are usually dispersed by wind, attachment to animals, or gravity, while species with larger seeds are mostly dispersed by vertebrates (Hughes et al., 1994). Moreover, species with small seeds tend to have short life spans (Thomson et al., 2005). Even though small seed sizes are expected to increase range shifts, Thomson et al. (2005) found that seed mass is positively correlated with dispersal distance itself, meaning that larger seeds would disperse further. This correlation was found within ballistic (dispersal through an explosion of the fruit which ejects the seeds), unassisted and wind dispersed species. However, plant height had a stronger effect on seed size, and when adjusting for plant height seed mass had very little effect (Thomson et al., 2005). Since seed mass is linked to these other traits, it should be expected if one of these influences range size, others may as well. Similarly, if significant effects of seed mass are found, different factors may explain the variation more strongly.

What is the evidence of the effect of dispersal traits on range shifts?

In this paper, 10 studies are reviewed to examine which dispersal traits may influence range shift ability (see table 1 in annex). In most studies reviewed, seed dispersal mechanism had a significant effect on range shifts. For example, Holzinger et al (2007) found that species with wind dispersal had larger range shifts. Similarly, Dullinger et al. (2012), found that gut survival probability (measuring endozoochory) and attachment to animal fur (measuring exozoochory) increased range filling, and Van der Veken et al. (2007) found the same for species with anemochory, endo- and exozoochory compared to mechanisms that transport over smaller distances. These results seem to indicate that dispersal modes that facilitate greater seed transport distances (anemochory, zoochory) increase range shift ability. However, Angert et al., (2011) found no significant effect, and Felde et al. (2015) found that species with boiochorial dispersal (dispersal where seeds shoot away from the plant via an explosive mechanism and are then dispersed by wind) had a larger range shift, even though seeds with boiochoric dispersal only disperse short distances (Vittoz & Engler, 2007).

Studies usually report these dispersal modes in categories, where all species with a certain dispersal mode are investigated together. Although this is a convenient method to use for testing, species with the same dispersal mode can differ strongly in their dispersal distance (Thomson et al., 2005).

For example, within dispersal by wind (anemochory), plants have diaspores with various appendages that help dispersal, such as a pappus, wings or no structures (Parolo & Rossi, 2008). Using dispersal modes as a categorical trait therefore disregards a considerable part of the information that is available. Dullinger *et al.*, 2012 was the only study where dispersal modes were measured as continuous variables. Here, gut survival probability and attachment to animal fur were measured based on regressions made by Römermann *et al.* (2007) and Mouissie (2004), which relate seed mass to gut survival and seed mass and diaspore structure to detachment rates. How dispersal modes are defined matters greatly for the results. For example, Holzinger *et al.*, (2007) made a dataset of changes in plant communities in the Swiss alps by comparing recent and historical data, which Angert *et al.* (2011) used again for a different analysis of traits. Holzinger *et al.* found a significant effect of anemochory on range shifts while looking at autochory, anemochory and zoochory. Angert *et al.*, however, comparing gravity to all other, further reaching, dispersal modes found no significant effect. This example indicates the importance of defining groups as homogenous as possible.

Most of the studies that measured the effect of either seed size, seed weight, or diaspore weight, found no significant effect (5 out of 7 studies). Only Parolo & Rossi (2008) and Wolf *et al.* (2016) found a negative effect on range shift ability of diaspore weight and seed size, respectively. Because seed mass is connected to several other life history traits that may affect range shift ability, such as life span (annual, perennial) and dispersal mechanism (anemochory), other factors might (also) be causally related in case positive correlations are found. Differences may also be caused by different locations. Since most research is done on elevational range shifts (table 1 in annex), there is a strong bias towards mountainous plant communities, meaning that results may differ in other areas.

Can information from other metrics, such as range size and range filling, give information about the effect of dispersal traits on future range shifts?

As shifts in distributions are difficult to determine, due to the lack of historical data to compare the current species ranges to, relatively few studies have researched the effect of dispersal traits on range shifts (Estrada *et al.*, 2016; Maclean & Beissinger, 2017). As a consequence, hypotheses are often derived from other fields of study that deal with the colonization and establishment of plants in new areas, such as how plant traits affect range size, range filling and invasion potential (Estrada *et al.*, 2016). These fields often have considerably more data available, and therefore traits that have proven to be important in these fields, may help predict future range shifts.

However, some debate is still going on about the accuracy of range size and range filling as proxy for range shifts. Traits effective in increasing the range size of plant species may indicate a good ability to colonize and establish populations in new areas, thereby expanding its range (Estrada *et al.*, 2016). However, dispersal characteristics would mainly increase range size if there is a time constraint, which causes species with limited dispersal distance to be unable to reach large range sizes. In Europe, it has been suggested that the last glacial period causes this time constraint, and that species have not yet reached their full potential range due to slow migration (Dullinger *et al.*, 2012). Since the last glacial period occurred several thousand years ago, this would indicate that plants only move ranges very slowly (Dullinger *et al.*, 2012). This does not correspond with evidence suggesting that plant communities already adjust to climate change within centuries, because of changes in species' regional abundances, as well as the arrival of new species (Shuman *et al.*, 2004).

The same problem applies to studies of range filling. Range filling is measured as the proportion of the potential range, based on abiotic factors, that species actually occupies (Estrada et al., 2016). If a species only occupies a small proportion of its potential range, it may be excluded by factors such as biotic interactions or dispersal limitation. Vulnerability to these factors may also reduce its range shift ability in the future (Estrada et al., 2016). However, similar to range size, during long time periods also poorly dispersing plants may have reached their full range, reducing the effect dispersal may have on current range fillings.

Concluding remarks

To understand and be able to predict the range shifts of plants, a thorough understanding of plants dispersal ability is crucial. However, since exact data on the dispersal ability is often not available, studies often use simple characteristics of plants, such as seed size and dispersal method, to determine dispersal capacity (Vittoz & Engler, 2007; Estrada et al., 2016). A recent review has investigated the effect of different plant traits on range shift ability, including dispersal, by noting which studies found positive effects (Estrada et al., 2016). However, noting which studies find positive effects may have limited use, because of the wide variety of different characteristics used to determine dispersal potential. Therefore it's important to evaluate which characteristics can estimate the real dispersal distance best, and what evidence exists that these characteristics influence range shift ability. Many studies which are reviewed in this paper researched whether plants with certain dispersal modes shift their range further. Most studies found a positive effect of long distance dispersal mechanisms (anemochory, zoochory) compared to mechanisms where seeds disperse close to the parental plant (see table 1 in annex). Dispersal mode therefore seems to influence range shift ability. Seed size, however, most often did not significantly correlate with the speed of range shifts, or range size and range filling, and therefore seems to be less valuable for predicting the future range shifts of plant species.

Some factors may diminish the effect of dispersal on range shift ability, or make it harder to detect differences. Firstly, besides dispersal, other plant traits may influence the ability to reach new places and survive there as well (Maclean & Beissinger, 2017). For example, there is evidence that ecological generalization influences range shifts, because species that are able to live in a wide variety of circumstances, may be more likely to find suitable habitat when expanding its range (Angert et al., 2011). Similarly, species with fast life histories (high reproduction and short life cycles) may establish new populations more quickly (Maclean & Beissinger, 2017). If one of these traits influences range shift ability strongly, this may make it more difficult to detect the effect of dispersal ability on range shifts. A meta-analysis would provide more information about the strength of each of these characteristics, and thereby may provide insight as to which are most important.

Secondly, new populations beyond the range limit may also be established by rare long distance dispersal events, in which seeds disperse large distances away from the parental plant. Because these events are rare (<2-10%) and highly stochastic, their importance is hard to determine (Corlett & Westcott, 2013). However, long distance dispersal may be important in rapid range shifts. Moreover, when populations need to pass unsuitable habitat to reach new suitable areas, the seeds may need to disperse over large distances (Dullinger et al., 2012). Long distance dispersal may in certain cases cause establishment of new populations beyond the current range limits, possibly above speeds that would be expected when only regular dispersal distances are considered.

However, seeds will have difficulty establishing in areas with closed vegetation, and it's not known how important these events are in nature (Vittoz & Engler, 2007).

Range shifts of plants are often difficult to determine, because of a lack of historical data about species distributions. However, traits that have been proven to increase range size and range filling may be good indicators for which traits increase range shift ability (Estrada et al., 2016). Next to dispersal mode and seed mass, other dispersal traits, such as diaspore morphology and ability to self-fertilize, could influence range shifts as well. To be able to compare studies, it's important that similar traits are used to determine the dispersal distances of seeds of different species, and that these traits reflect the true dispersal distances as closely as possible. Combining different fields of studies may help to determine whether dispersal characteristics affect range shifts, and thereby help predict which species may face extinction because of climate change, and what future ecosystems may look like.

Sources

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Annex

Tabel 1: the reviewed studies on the effect of dispersal traits on range shift, range filling or range size. Each dispersal trait measured within the study is represented in the table, including a description of the trait and whether it had a significant effect. The table includes studies researching range shifts at upper and lower range limit and optimal elevation.

<i>Species</i>	<i>Number of species studied</i>	<i>Area</i>	<i>Dispersal traits studied</i>	<i>Description of traits</i>	<i>Type of range shift/size/filling measured</i>	<i>Effect on range shift/size/filling</i>	<i>Type of study</i>	<i>Notes</i>	<i>Reference</i>
<i>Trees</i>	92	United States	Seed size	Seed per pound in an average seed lot	Shift of upper and lower latitudinal limit	No effect	Difference in adult and seedling distribution		Zhu et al., 2012
			Seed spread rate	Capability to spread compared to other species with the same growth habit (slow, moderate, fast)		No effect			
<i>Vascular plants</i>	52	Italian Alps	Diaspore weight	Divided into 5 weight classes; > 1.00; 0.50 < X ≤ 1.00; 0.10 < X ≤ 0.50; 0.01 < X ≤ 0.10; << 0.01	Shift of upper elevational limit	Marginally negative effect (p=0.058)	Comparing historical and current records	Effect of traits measured between slow and fast migrants	Parolo & Rossi, 2008
<i>Alpine plants</i>	133	Swiss alps	Diaspore morphology	No structure, wings, parachutists or spores		No effect	Comparing historical and current records	Same dataset as Holzinger et al., 2007	Angert et al., 2011
			Seed mass	Mass of one seed	Shifts of upper elevational limit	No effect			
			Seed dispersal mode	Gravity compared to further reaching dispersal modes		No effect			
			Duration of seed dispersal	Number of months between first and last reported seed shed		Marginally positive effect			
			Average height at seed shed			No effect			
			Breeding system	Obligately outcrossing, mixed mating and autogamously selfing		No effect			

Plants	106	Norway	Dispersal mechanisms	wind (boleochory, meteorochory), animal (endochory, epichory, dysochory, myrmekochory), human (anthropochory), water (hydrochory) and self- dispersal (autochory)	Shifts at upper and lower elevational limit and species optima	Species with boleochorial dispersal shifted their optima more upwards	Comparing historical and current records		Felde et al., 2012
Plants	4426	California	Seed size	Divided in the groups; small seeds (1000-wt < 0.1 g), medium seeds (0.1 g ≤ 1000-wt < 10 g), large seeds (1000-wt ≥ 10 g)	Shift of upper and lower elevational limit	Negative	Comparing historical and current records	Compared to null model small seeds shifted more, but no sign. differences between seed size groups	Wolf et al., 2016
Alpine plants	133	Swiss alps	Dispersal mode	3 categories; Anemochory, autochory and zoochory	Shift of upper elevational limit	Anemochorous species shifted their range further	Comparing historical and current records	Same dataset as Angert et al., 2011	Holzinger et al., 2007
			Diaspore length	1,6 mm or smaller compared to larger than 1,6 mm		No effect			
			Dispersal timing	In which month the species disperses their seeds		No effect			
Alpine plants	101	Swiss alps	Reproduction type	Sexual only; mainly sexual rarely vegetative; sexual and vegetative; mainly vegetative rarely sexual	Shift of upper elevational limit	No effect	Comparing historical and current records	(Partly) same historical data as Holzinger & Angert	Vittoz et al., 2009
			Pollen vector	Selfing (including cleistogamy and geitogamy); wind; insects only; insect and selfing		No effect		Compares strong and weak colonizers	
			Diaspore weight	Weight of one diaspore in mg		No effect			
			Potential dispersal distance	Short, medium, long (simplified from Vittoz & Engler, 2007)		Negative effect			
			Dispersal vector	Anemochory or zoochory		No effect			

			<i>Diaspore morphology</i>	<i>Fleshy fruits; pappus; wings or fringes; awn, hooks or calyx; no appendage</i>		<i>Species with pappus or wings shifted their range further</i>		
<i>Plants</i>	1276	Europe	Seed mass	Mass of one seed	Range size and range filling	No effect	Same traits were sign. for range size and range filling	Estrada et al., 2015
			Dispersal distance	Categories made according to Vittoz & Engler (2007)		Positive		
			Seed bank persistence	The period for which seeds persist in a viable state in the soil		Positive		
			Capacity to self-fertilize			No effect		
			Flower pollinator	External pollinators (insects or wind/water) or self-pollination		No effect		
			Age of first flowering			Positive		
			Reproductive frequency			No effect		
<i>Vascular plants</i>	111	Austrian alps	Seed terminal velocity	Maximum speed of the seed while falling down	Range filling	Negative		Dullinger et al., 2012
			Gut survival probability	Based on a regression relating seed mass to gut survival		Positive		
			Attachment to animal fur	Based on a regression relating seed mass and surface structure to detachment rates		Positive		
<i>Forest herb species</i>	273	Europe (NL, BE, LU, FR, DL)	Diaspore weight	Weight of one seed in mg	Range size	No effect		Van der Veken et al., 2007
			Seed size	Average of seed length, width and thickness in mm		No effect		
			Seed production	5 classes: 1, < 25; 2, 26–100; 3, 101–1000; 4, 1001–10,000; 5, > 10,000		Positive		
			Dispersal types	Anemochory; endozoochory and exozoochory;		Anemochory & endo- and exozoochory		

	<i>Dispersal types</i>	<i>Anemochory; endozoochory and exozoochory; ballistochory, myrmecochory and barochory; hydrochory</i>	<i>Anemochory & endo- and exozoochory increased range sizes</i>
	Seed bank longevity index	Proportion (%) of short- and long-term persistent records on total	Positive