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Drivers of plant species' potential to spread: the importance of demography versus seed dispersal

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(Abstract)

Understanding the ability of plants to spread is important for assessing conservation strategies, landscape dynamics, invasiveness and ability to cope with climate change. While long-distance seed dispersal is often viewed as a key process in population spread, the importance of inter-specific variation in demography is less explored. Indeed, the relative importance of demography *vs* seed dispersal in determining population spread is still little understood. We modelled species' potential for population spread in terms of annual migration rates for a set of species inhabiting dry grasslands of central Europe. Simultaneously, we estimated the importance of demographic (population growth rate) *vs* long-distance dispersal (99th percentile dispersal distance) characteristics for among-species differences in modelled population spread. In addition, we assessed how well simple proxy measures related to demography (the number and survival of seedlings, the survival of flowering individuals) and dispersal (plant height, terminal velocity and wind speed during dispersal) predicted modelled spread rates.

We found that species' demographic rates were the more powerful predictors of species' modelled potential to spread than dispersal. Furthermore, our simple proxies were correlated with modelled species spread rates and together their predictive power was high. Our findings highlight that for understanding variation among species in their potential for population spread, detailed information on local demography and dispersal might not always be necessary. Simple proxies or assumptions that are based primarily on species demography could be sufficient.

Introduction

Understanding the ability of species' populations to spread in space is important in determining their invasiveness (Neubert and Parker 2004, Lewis et al. 2006). Reliable information on spreading capability is also crucial for conservation management at the landscape scale (Bullock et al. 2002) and strategies to mitigate declines in native species (Le Corff and Horvitz 2005). Assessing potential population spread rates has become of particular interest in the context of climate change, whereby species' may have to shift their ranges rapidly to track suitable habitat (Nathan et al. 2011a, Bullock et al. 2012, Harsch et al. 2014).

Dispersal is often viewed as a key driver of species' spread and colonization, with long-distance dispersal being seen as an especially important process (Higgins and Richardson 1999, Neubert and Caswell 2000, Coutts et al. 2011). However, effective dispersal in plants (Schupp et al. 2010) can only occur where a sufficient amount of propagules (hereafter seeds) disperse and establish to allow populations to grow. Several studies have suggested that variation in demography (i.e. in local population dynamics) could have a greater impact on species' spread than dispersal (e.g. Nathan et al. 2011a, Hemrova et al. 2012, Vazacova and Munzbergova 2014), although others have found the opposite (Coulson et al. 2001, Bullock et al. 2008). The demography of a plant species influences dispersal in terms of the number of seeds available to disperse. One might thus expect higher spread rates in species producing more seeds. However, populations need to grow following dispersal to allow populations to exist at all, hence including (positive) population growth rates in assessing spreading capacity is of major importance. Although species producing more and smaller seeds (Westoby et al. 1992) can disperse longer distances (Tamme et al. 2014), they could suffer from higher seed and post-recruitment mortality (Moles and Westoby 2004). Therefore their spread through landscapes may ultimately be slower than that of larger seeded species which have shorter dispersal but better survival. Addressing how such opposing drivers play out for different species' spread rates is hindered by scarcity of studies that assess dispersal and demography across multiple species.

Covering this gap, the first aim of this study is to assess the relative importance ("power") of local demography and dispersal ability in explaining differences among species in their potential to spread in the landscape. To do so, we first estimated species' spread potential using the analytical wavespeed (stage-structured integrodifference equation) model of Neubert and Caswell (2000), which requires information on demography and dispersal. Thanks to its simplicity, this model has often been used to assess population spread (e.g. Neubert and Parker 2004, Buckley et al. 2005, Skarpaas and Shea 2007, Soons and Bullock 2008, Bullock et al. 2012). However, the model needs detailed information describing

the dispersal kernel and the population demographic matrix. The need for detailed information on both demography and dispersal restricts the number of species which can be modelled. Our second aim is therefore to examine whether differences in potential spread rates among species can be predicted using simple plant characteristics or if detailed information on dispersal and demography are always necessary.

We calculated potential spread rates for a set of species inhabiting dry grasslands in central Europe. We considered this habitat type as a model system which allows us to focus on inter-specific differences rather than those due to large-scale environmental gradients. To fulfil the second aim, we selected several simple characteristics related to seed dispersal and demography. For dispersal characteristics we focused on plant height, seed terminal velocity and wind speed during the dispersal season as essential parameters for wind dispersal (Katul et al. 2005). Characteristics related to demography were chosen to be, in general, relatively easy to measure in the field (although, in our study we derived them from population demographic matrices). These characteristics comprise the number of seedlings as a simple proxy of reproductive success, and survival of seedlings and of flowering individuals as measures of longevity (Silvertown et al. 1993).

Materials and methods

Modelled species

We selected sixteen species for this study (Table 1), using the following criteria. First, all species inhabit calcareous dry grasslands (alliance *Bromion erecti*, Ellenberg 1988), which are typical of the fragmented agricultural landscape of northern Bohemia in the Czech Republic. We refer to Knappova et al. (2012) for more details on the study landscape. These grasslands have been used as a model system in several studies of species' landscape-level dynamics and distribution (Munzbergova 2004, Tremlova and Munzbergova 2007, Chylova and Munzbergova 2008, Hemrova et al. 2012, Knappova et al. 2012), because they are species-rich, host both rare and common species, have a diverse land-use history and vary strongly in species composition. A list of species inhabiting these dry grasslands has been published in Hemrova and Munzbergova (2015). Second, each species has at least one field-derived demographic matrix (having population growth rates >1, as the wavespeed calculation requires a growing population) gathered by group members (Eriksson and Eriksson 2000, Lofgren et al. 2000, Kiviniemi 2002, Munzbergova 2005, 2006, 2007, Cerna and Munzbergova 2013, Munzbergova 2013, Koubek unpubl. data and Rothanzl unpubl. data), or available in the COMPADRE Plant Matrix Database (Salguero-Gomez et al. 2015). In cases where more than one matrix was available for a species (Supplementary

material Appendix 1, Table A1), we calculated a single mean matrix. For more details on such mean matrices we refer to Supplementary material Appendix 1, A1. The selected species differ in their life histories, seed release periods and plant heights (Table 1, Supplementary material Appendix 1, Table A1). Most of these species do not have any dispersal structures or have a pappus and thus are expected to be primarily dispersed by wind.

Determinants of species' potential to spread

To assess which of the species dispersal or local demography is more important in modelled species' potential to spread, we assembled "composite characteristics" that summarise these variables. Dispersal ability (Ddist; Table 1,2) was calculated as the 99th percentile distance of the dispersal kernel. We used the WALD model (Katul et al. 2005) to derive wind dispersal kernels for each species, following the methods described in Bullock et al. (2012; see Supplementary material Appendix 1, A2 for details on the modelling of wind dispersal). The mechanistic WALD model uses plant characteristics of seed terminal velocity and release height as well as environmental information on wind speed and turbulence. We modelled only dispersal by wind, since wind is the only dispersal vector for which dispersal kernels can be derived mechanistically (Nathan et al. 2011b). Simulation approaches exist for animal vectors (Cortes and Uriarte 2013), but these require detailed measures of the animal movement paths, seed retention, etc. This decision is also justified by the fact that in this landscape wind is a major dispersal vector (Tremlova and Munzbergova 2007). Furthermore, some of our species have clonal reproduction, but to model species' dispersal we considered only that by seed as clonal dispersal is not long-distance dispersal. The demographic matrix was summarized in terms of the population growth rate (λ; Table 1,2), which is dependent on the demographic plant traits (survival, growth and fecundity of individuals). Dispersal distance and population growth rate are further utilised as composite characteristics.

We also used individual characteristics that contribute to local demography and could be derived from the matrices. These were: seedling production per flowering individual (Sprod), survival of seedlings (Ssurv) and of flowering individuals (Fsurv). Similarly, we calculated simple proxies of dispersal ability by wind: terminal velocity (Vterm), seed release height (Pheight) and wind speed (Windsp; Table 1,2). Although wind speed is not a species characteristic per se, it is used here as indirect characteristic. Here, wind represents the variation in wind speeds encountered over the period of seed release, which varies among species. The values for seed release heights and terminal velocities originate from Tremlova and Munzbergova (2007) and Hemrova and Munzbergova (2015). Wind speeds were the maximum daily wind speeds as detected at 10 m height by the Czech Hydrometeorological Institute at the

meteorological station near to the study area in Doksany from 1971 to 2010. Data from a longer time period allowed us to estimate average wind conditions and to reduce the effects of rare extreme values. Detailed exploration of the dispersal data suggested that wind conditions were relatively stable among years. We calculated mean daily maximum wind speed for each species during its dispersal period based on wind speed data from 1971 to 2010. We assumed that the dispersal period started in the middle of the period of flowering and ended a quarter of the flowering period after flowering has ceased (Supplementary material Appendix 1, Table A1).

Modelling population spread

To model species' potential spread rates we used the analytical wavespeed model of Neubert and Caswell (2000) which is an integrodifference equation combining a demographic matrix with a dispersal kernel. Another possibility would be to use a spatial integral projection models (Jongejans et al. 2011), which allow assessing the importance of individual demographic variation. Moreover, integral projection models have been shown to outperform matrix models for small datasets (Ramula et al. 2009). However, integral projection models require access to the raw demography data, which are unavailable for many species, strongly restricting species choice. In contrast, population demographic matrices, which are necessary for integrodifference equation models, are more widely available (Salguero-Gomez et al. 2015).

The wavespeed model of Neubert and Caswell (2000) simulates a population spreading in one dimension from a starting location in discrete time steps. This approach allows stage-structured demography and realistically complex dispersal kernels, but includes simplifying assumptions such as no temporal variation or Allee effects and a spatially homogeneous environment. Although simple, it is a general approach to modelling the population spread into unoccupied habitats (e.g. Skarpaas and Shea 2007, Bullock et al. 2008, Soons and Bullock 2008). According to Neubert and Caswell (2000) population density at location x at time $t + 1$ is defined as

$$\mathbf{n}(x, t+1) = \int_{-\infty}^{\infty} \left[\mathbf{K}(x - y) \circ \mathbf{B_n} \right] \mathbf{n}(y, t) \mathrm{d}y ,$$

where $\circ$ is the Hadamard product operator, $\mathbf{B_n}$ is a stage-structured population projection matrix describing density-dependent population growth at location y, $\mathbf{K}(x - y)$ is a matrix of dispersal kernels describing the set of probabilities of the relocation from y to x of individuals undergoing each demographic transition, with the assumption that dispersal from y to x depends only on the relative locations of the two points.

Calculation of the wavespeed requires a projection matrix representing demography at low density (i.e. at the forefront of the spreading population; $\mathbf{A} = \mathbf{B}_0$), and all species' matrices followed this requirement by having population growth rates >1 (Table 1, Supplementary material Appendix 1, A1). A further matrix $\mathbf{M}(s)$ describes the dispersal kernel for each demographic transition in terms of a moment generating function (MGF). The WALD model has an analytical MGF and thus dispersing elements of the matrix $\mathbf{M}(s)$ are as follows

$$m_{ij}(s) = \exp\left[\frac{\lambda'(u)}{\mu'(u)}\left(1 - \sqrt{1 - \frac{2\mu'(u)^2 s}{\lambda'(u)}}\right)\right],$$

where s describes the shape of the population wave (Neubert and Caswell 2000); for non-dispersing transitions $m_{ij}(s) = 1$. Under this model a population forms a wave of a constant shape that advances at constant speed c^* (the wavespeed), which can be derived analytically by

$$c^* = \min_{s>0}\left(\frac{1}{s}\ln \rho(s)\right),$$

where ρ is the dominant eigenvalue of $\mathbf{A} \circ \mathbf{M}(s)$. All the calculations were performed in Matlab 7.0.4.365.

Data analysis

We tested for correlations among individual and among composite species' characteristics related to dispersal and demography using Spearman rank tests (for correlations, see Supplementary material Appendix 1, Table A2). Characteristics were not significantly correlated except in one case and the correlation was not strong ($r < 0.6$ in all cases). Therefore we included all characteristics in subsequent tests. Importantly, the composite characteristics for population growth (λ) and dispersal ability (Ddist) were not correlated.

The ability of the characteristics to predict the species' potential to spread was tested with a linear regression. Natural logs of the wavespeed values were employed to improve normality in the data. To avoid overfitting due to the relatively high number of tested variables together with our relatively small dataset, we regressed each individual characteristic (i.e. Sprod, Ssurv, Fsurv, Pheight, Vterm, Windsp; Table 3) on wavespeed separately. Subsequently, we selected the significant characteristics using Akaike information criterion (AIC) and included them in one model to assess their relative importance for wavespeed. The same method was done separately for composite characteristics (i.e. λ and Ddist; Table 3) and the analyses of individual vs. composite characteristics were compared. The values of Sprod, λ and

Ddist were logarithmically transformed to reduce the effects of extreme values in the analyses. All the analyses were performed using R 3.0.2 (R Development Core Team 2013).

Results

Calculated wavespeeds ranged from 0.006 m.yr^{-1} (*Plantago media*) to 1.184 m.yr^{-1} (*Linum catharticum*), mean = 0.329 m.yr^{-1}. The single regressions of individual characteristics showed seedling production, survival of flowering individuals, plant height and wind speed as having a significant relationship with wavespeed (Table 3, Fig. 1). However, when used in a single model, only three of them (seedling production, survival of flowering individuals and plant height, but not wind speed) made a significant contribution to the model. All selected individual characteristics together explained 73 % of variability in the data. Seedling production had the highest explanatory power ($R^2 = 33$ %) among all characteristics (Table 3). From the two composite characteristics both λ and Ddist had a significant relationship with wavespeed (Table 3). When used in a single model, they explained 56 % of variability in the data, with λ explaining almost twice as much variation as Ddist (R^2: 0.46 vs. 0.28).

Discussion

The study found that species' demography was more important than dispersal in explaining inter-specific variation in the modelled potential to spread in the landscape. Both individual and composite demographic characteristics had greater importance in the regressions on wavespeed compared to dispersal characteristics. Such a finding may appear counter-intuitive as dispersal, especially long distance dispersal, has been largely accepted as critical driver of population spread (e.g. Clark 1998, Higgins and Richardson 1999, Bullock and Clarke 2000). Our study is not contradictory in that it does show dispersal is a predictor of species' potential to spread. However, the species demography after dispersal seems an even more powerful predictor. Such strong impacts of demographic variation on species' large-scale dynamics have been suggested in other studies (e.g. Clark et al. 2001, Pergl et al. 2011, Hemrova et al. 2012), although these did not make formal comparisons with dispersal. Nathan et al. (2011a) came to a similar conclusion about a larger impact on spread rates of inter-specific variation in demography than in dispersal using a different approach to ours in modelling spread of 12 North American trees. In contrast, considering large-scale variation in demography and dispersal within a single invasive *Carduus* species, Jongejans et al. (2008) found dispersal made a greater contribution to the wavespeed.

Our composite descriptor of demography, the population growth rate λ, showed much less variation than the descriptor of dispersal, the 99th dispersal percentile Ddist, suggesting our finding is not a statistical artefact. Both descriptors are well known standards, with λ being the dominant eigenvalue describing the demographic matrix and the 99th percentile being an accepted measure of long-distance dispersal (Caswell et al. 2003, Tamme et al. 2014). Demography and dispersal jointly drive the spatial population dynamics of species, but our finding of an enlarged importance of demography emphasizes that to allow spread of a species through landscapes, dispersal must be followed by the successful establishment, growth and reproduction of plants (Schupp et al. 2010).

Another conclusion of our study is that some species' individual characteristics such as lower survival of flowering individuals, but especially higher seedling production, i.e. characteristics related to demography, can indicate the ability to spread. Both lower survival of flowering individuals and higher seedling production is indicative of the rapid growth, high reproductive life cycle characterized along the fast-slow continuum (e.g. Salguero-Gomez et al. 2016) and so might be expected to be related to increased population spread rates. Our study also showed that detailed information on local population dynamics and dispersal may not be needed to estimate inter-specific variation in spread; the individual characteristics explained a high amount of variation in the wavespeeds. Various plant characteristics have been repeatedly proved to be useful indicators of species landscape-level dynamics and distribution (e.g. Dupre and Ehrlen 2002, Verheyen et al. 2004, Lindborg 2007, Tremlova and Munzbergova 2007, Hemrova and Munzbergova 2015), in this study we found that they are also good estimates of modelled species potential to spread.

Species spread across landscapes

We found that wavespeeds ranged between 0.006 and 1.184 m.yr^{-1} in the studied grassland species. Such spread may seem slow, but similar modelled wavespeeds are not exceptional among plant species (see e.g. Neubert and Caswell 2000, Neubert and Parker 2004, Bullock 2012, Bullock et al. 2012). Wavespeed can accurately predict population spread rates if dispersal and demography are measured so that they represent the modelled system well (e.g. Bullock et al. 2008). While Neubert and Caswell (2000) found the discrepancy between real and modelled spread rates for teasel (due to poor dispersal data), Caswell et al. (2003) found good agreements between modelled and empirical spread rates for sparrowhawk, pied flycatcher and starling.

One might expect that species with higher wavespeeds, i.e. a higher modelled potential to spread, would be more frequent in our grassland landscape. The contrary might be explained by unavailability of

habitats suitable for the species. Four of the nine species with a higher wavespeeds (> 0.25 m.yr^{-1}) are relatively common in the study landscape (Hemrova and Munzbergova 2015). These species (*Anthyllis vulneraria*, *Carlina vulgaris*, *Falcaria vulgaris* and *Linum catharticum*) are rather short-lived (Supplementary material Appendix 1, Table A1), which is in accord with our earlier comment concerning increased population spread rates in species with the rapid growth along the fast-slow continuum. The remaining five species (*Anthericum ramosum*, *Cirsium pannonicum*, *Linum flavum*, *Linum tenuifolium* and *Scorzonera hispanica*) are rare, being found in 1 to 7% of dry grasslands in the study landscape. These species tend to occur in older grasslands (Hemrova and Munzbergova 2015). This might seem surprising as a higher potential to spread might be expected to affect species' distributions positively. In our previous study Hemrova and Munzbergova (2015) we suggested that certain species primarily occupy older grasslands because of their different habitat quality, i.e. they are habitat rather than colonization limited. Habitat limitation could thus explain rarity of those species with higher modelled potential to spread in landscape, but suggests such species may respond well at a landscape scale to habitat restoration or other positive environmental changes.

Among the remaining seven species with wavespeed < 0.25 m.yr^{-1} there are both rather rare species with incidence from 5 to 15% in the study landscape (*Aster amellus*, *Aster linosyris* and *Trifolium montanum*) and common or very frequent species (29–92% of dry grasslands in the study landscape; *Agrimonia eupatoria*, *Cirsium acaule*, *Plantago media* and *Primula veris*); the lowest wavespeed was found for *Plantago media* which is quite frequent occupying 66% of dry grasslands in the landscape (Hemrova and Munzbergova 2015). Hence species with low modelled wavespeeds belong to the most frequent species in the landscape. As was suggested above, species occurrence seems to be the result of habitat limitation rather than the result of dispersal ability. In our study, species with low modelled wavespeeds but high frequencies in the landscape have many available and less isolated habitat patches. Giving enough time those species can slowly colonize the whole landscape. Time is especially important for species with slow landscape-level dynamics to obtain an equilibrium occurrence in a landscape as was shown by Herben et al. (2006). Such species tend to more slowly react to environmental changes. Under climate change we might expect these to have greater problems to track shifting suitable habitat. On the contrary, these species are also long-lived and often clonal, which lower their probability to go rapidly extinct in unsuitable environments and enhance the possibility to survive such conditions for longer time while slowly colonizing more suitable habitats.

Model uncertainties

The aim of this study was to understand how inter-specific variation in dispersal and demography drives differences in the potential ability to spread, calculated in terms of the wavespeed. Species in this study vary in plant height, seed terminal velocity, dispersal season, life history type and in the transition values and dimensions of the demographic matrix. We have shown that in fact all combine in a complex fashion to affect the modelled wavespeed. Our aim was explicitly not to make precise predictions about the rate of spread of each species, but rather to construct realistic models based on good quality data allowing assessments of the determinants of wavespeed. Indeed, there are several reasons why the actual spread rates of our studied species would likely differ from the modelled values. Wavespeed values can change dramatically with the model parameters. Bullock et al. (2012) showed sensitivity of species spread to changes in wind speeds. In our study we used mean of daily maximum wind speeds from a nearby meteorological station measured over long 40-year period. Using the mean values and thus supressing the extreme wind speeds could cause the overall slower spread rates estimated for studied species. Terminal velocity and plant height also impact wind dispersal distances (e.g. Nathan et al. 2011a, Bullock et al. 2012). We have previously measured these parameters in the study landscape (Tremlova and Munzbergova 2007, Hemrova and Munzbergova 2015), so we can assume they are reliable. Therefore, the WALD dispersal kernels are likely a good representation of the ability of these study species to spread via wind across the study landscape. However, we would expect other vectors to disperse seeds in such systems, such as livestock, wild large herbivores and cutting machinery, and these may both decrease or increase dispersal distances (e.g. Bullock et al. 2008, Hemrova et al. 2012).

Concerning demography, for more than half of the studied species we had data for matrices obtained from the study landscape or nearby. Data for the other species were obtained from COMPADRE Plant Matrix Database (Salguero-Gomez et al. 2015) and represented a range of locations across central-northern Europe. Thus, the measured demography for these species do not relate to the region for which we obtained wind speed data. However, we follow the common assumption in comparative analyses that the demographic and dispersal differences among species are bigger than those among populations within species (e.g. Tamme et al. 2014, Salguero-Gomez et al. 2016). Moreover, even within a location, management has large effects on demography, which follows through to impact wavespeed (Bullock et al. 2008). In the study landscape, some of the grasslands are managed, some of them are not. Finally, the wavespeed model used here assumes the landscape over which the species' spread comprises homogenous suitable habitat for the species. In reality, habitat quality will vary greatly across a landscape (Gilbert et al. 2014). Indeed, making precise predictions of rates of spread is fraught with difficulties in

terms of data and models (Nathan et al. 2011a, Bullock et al. 2012, Santini et al. 2016). However, we consider the method and data sufficient for the aims of this study; we used the best available demographic data for these species, alongside mechanistic calculations of dispersal kernels and a mathematically rigorous model for spread rates.

Conclusions

Our study found species' demography to be the more powerful driver explaining the modelled potential of species to spread in landscape compared to dispersal ability. While dispersal is often viewed as a key process in population spread, the importance of inter-specific variation in demography after the dispersal event should not be underestimated. Our findings also suggest that to estimate species' potential for population spread, detailed information on local demography and dispersal might not always be necessary. More simple proxies based on demography and dispersal could be sufficient. Among the species' characteristics used in this study, seedling production proved to be the best indicator of species' potential to spread. As the individual characteristics are not hard to obtain compared to detailed information on demography or dispersal, it could make predictions of patterns in species' potential to spread considerably easier. It is important to keep in mind that our study is based on the comparison of sixteen dry-grassland species. Therefore, to make general conclusions about the importance of the individual characteristics to species' population spread is beyond the scope of this paper. To do so would require study of more species from different habitat types and with traits under different selection pressures.

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Table Legends

Table 1. The sixteen species selected for the study, the values of their dispersal and demographic characteristics and calculated wavespeeds.

Species	Species dispersal				Demography				Wavespeed
	Ddist [m]	PHeight [m]	Vterm [m.s^{-1}]	Windsp [m.s^{-1}]	λ	Sprod	Ssurv	Fsurv	[m.yr^{-1}]
Agrimonia eupatoria L.	2.142	0.617	2.827	8.352	1.007	0.213	0.613	0.998	0.038
Anthericum ramosum L.	2.535	0.641	2.808	9.013	1.255	2.197	0.723	0.905	0.319
Anthyllis vulneraria L.	1.885	0.285	1.564	9.356	1.415	6.677	0.257	0.175	0.512
Aster amellus L.	5.147	0.335	0.800	8.034	1.003	0.166	0.608	0.901	0.030
Aster linosyris (L.) Bernh.	1.541	0.369	2.120	8.352	1.174	0.829	0.149	1.000	0.084
Carlina vulgaris L.	4.318	0.355	0.995	8.352	1.069	2.133	0.853	0.000	0.466
Cirsium acaule (L.) Scop.	3.213	0.135	0.387	8.352	1.008	0.531	0.760	0.992	0.025
Cirsium pannonicum (L. fil.) Link	44.58	0.640	0.420	9.600	1.013	0.784	0.564	0.972	0.646
Falcaria vulgaris Bernh.	1.762	0.550	2.907	8.352	1.140	4.207	0.805	0.730	0.254
Linum catharticum L.	1.754	0.227	1.220	9.013	2.864	4.295	0.095	0.081	1.184
Linum flavum	2.164	0.377	1.910	9.356	2.714	111.7	0.222	0.874	0.863
Linum tenuifolium L.	1.385	0.235	1.500	9.013	1.318	5.120	0.463	0.732	0.296
Plantago media L.	0.961	0.268	2.091	8.352	1.003	0.186	0.200	1.000	0.006
Primula veris L.	0.457	0.200	3.101	10.316	1.121	14.74	0.586	1.000	0.034
Scorzonera hispanica L.	14.53	0.900	1.242	9.876	1.057	1.623	0.870	0.971	0.639
Trifolium montanum L.	1.842	0.378	2.070	9.013	1.054	1.447	0.529	0.951	0.117

Note: Ddist = Dispersal distance; Pheight = Plant height; Vterm = Terminal velocity; Windsp = Wind speed; λ = Population growth rate; Sprod = Seedling production;

Ssurv = Survival of seedlings; Fsurv = Survival of flowering individuals. The nomenclature follows Tutin, T. G. et al. (eds.) 1964–1983. Flora Europaea. – Cambridge

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Table 2. List of characteristics (their units and mean and range of their values) of 16 dry grassland species used in this study.

Characteristics	Mean	Range	Units
Species dispersal			
99th percentile dispersal distance (Ddist)	5.639	0.457–44.589	m
Plant height (Pheight)	0.407	0.135–0.900	m
Terminal velocity (Vterm)	1.748	0.387–3.101	m.s^{-1}
Wind speed (Windsp)	8.919	8.034–10.316	m.s^{-1}
Demography			
Population growth rate (λ)	1.326	1.003–2.864	
Seedling production (Sprod)	9.808	0.166–111.778	
Survival of seedlings (Ssurv)	0.519	0.095–0.870	
Survival of flowering individuals (Fsurv)	0.768	0.000–1.000	

Table 3. Impact of dispersal and demographic characteristics on species' spread potential (wavespeed). The effects of individual characteristics on wavespeed were first tested separately and then the significant ones (according to AIC) were combined in one model. The same was done for the composite characteristics. Significant relationships (positive ΔAIC) are highlighted in **bold**.

Individual characteristics	Individual tests				Selected characteristics			
	R^2	β	F	ΔAIC	R^2	β	F	ΔAIC
Demography								
Sprod	**0.329**	**+**	**8.364**	**5.494**	0.139	+	7.241	6.100
Ssurv	–0.071	–	0.001	–1.999				
Fsurv	**0.234**	**–**	**5.585**	**3.371**	0.271	–	13.129	10.570
Seed dispersal								
Pheight	**0.055**	**+**	**1.871**	**0.007**	0.296	+	14.273	11.31
Vterm	–0.026	–	0.613	–1.314				
Windsp	**0.114**	**+**	**2.934**	**1.044**	–0.021	+	0.050	–1.920
All selected					0.732		11.243	18.036
Composite characteristics								
Demography – λ	**0.286**	**+**	**6.999**	**4.487**	0.460	+	15.652	10.650
Seed dispersal – Ddist	**0.100**	**+**	**2.665**	**0.788**	0.275	+	9.738	6.950
All selected					0.560		10.553	11.440

Note: We show adjusted R^2 for all tests. β = regression coefficient; ΔAIC = improvement in AIC between tested models. Sprod = Seedling production; Ssurv = Survival of seedlings; Fsurv = Survival of flowering individuals; Pheight = Plant height; Vterm = Terminal velocity; Windsp = Wind speed; λ = Population growth rate; Ddist = Dispersal distance.
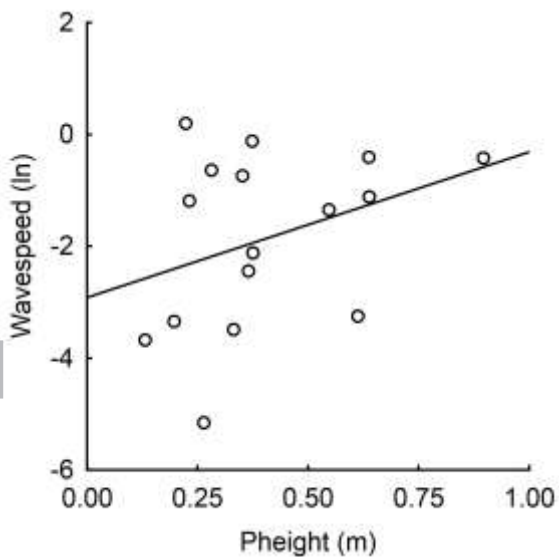
Figure Legend

Fig. 1. Effects of A) seedling production, B) plant height and C) wind speed on wavespeed in regression
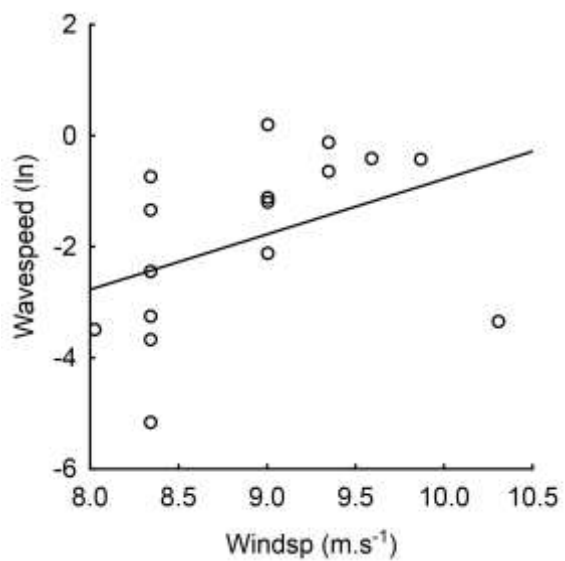
model.

A)
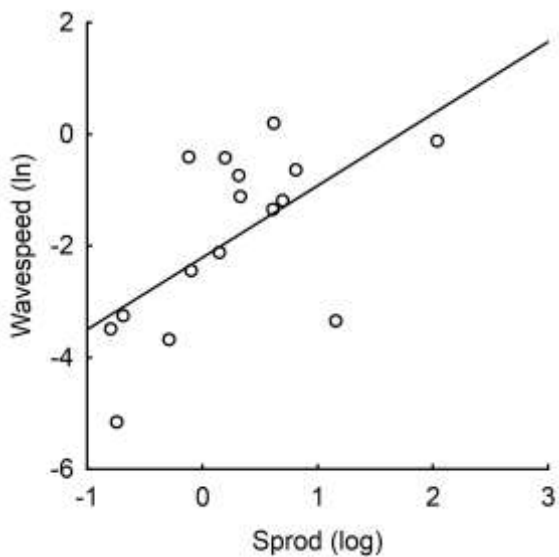
B)

C)

3

4   **Table A1**. The sixteen species selected for the study; their family, life history, dispersal structures on diaspores, start and end of seed release

5   period, the number of matrices used for calculation of a mean matrix, the number of stages in the demographic matrix, presence of a clonal stage

6   in the matrix, country in which the demography was measured, source of the demographic matrix.

Species	Family	Life history[†]	Diaspore structures[†]	Seed release period[†]* (month)	Matrix properties				
					No. used matrices	No. stages	Clonal stages	Origin	Source
Agrimonia eupatoria	Rosaceae	P	Hooks	VIII–X	9	4	No	SE	(Kiviniemi 2002)
Anthericum ramosum	Asparagaceae	P	None	VII–IX	12	8	Yes	CZ	(Cerna and Munzbergova 2013)
Anthyllis vulneraria	Fabaceae	B, P	None	VII–VIII	1	4	No	FR	(Bastrenta et al. 1995)[‡]
Aster amellus	Asteraceae	P	Pappus	IX–XI	13	5	Yes	CZ	(Munzbergova 2007)
Aster linosyris	Asteraceae	P	Pappus	VIII–X	6	4	Yes	CZ	(Rothanzl unpubl. data)
Carlina vulgaris	Asteraceae	B, P	Pappus	VIII–X	3	3	No	SE	(Lofgren et al. 2000)
Cirsium acaule	Asteraceae	P	Pappus	VIII–X	8	4	Yes	CZ	(Munzbergova 2005)
Cirsium pannonicum	Asteraceae	P	Pappus	VI–VIII	6	4	Yes	CZ	(Munzbergova 2005)
Falcaria vulgaris	Apiaceae	B, P	None	VIII–X	13	3	No	CZ	(Koubek unpubl. data)
Linum catharticum	Linaceae	A, B, P	None	VII–IX	1	4	No	NL	(Verkaar and Schenkeveld 1984)[‡]
Linum flavum	Linaceae	P	None	VII–VIII	9	3	No	CZ	(Munzbergova 2013)
Linum tenuifolium	Linaceae	P	None	VII–IX	9	3	No	CZ	(Munzbergova 2013)
Plantago media	Plantaginaceae	P	None	VIII–X	1	5	No	SE	(Eriksson and Eriksson 2000)
Primula veris	Primulaceae	P	None	V–VI	1	6	No	SE	(Ehrlen et al. 2005)[‡]
Scorzonera hispanica	Asteraceae	P	Pappus	VI–VII	8	3	No	CZ	(Munzbergova 2006)
Trifolium montanum	Fabaceae	P	None	VII–IX	1	4	No	DE	(Schleuning and Matthies 2009)[‡]

7   Note: † assembled from Hejný et al. (1995–2010); * based on flowering period (start calculated as the middle of the flowering period, end as the end of flowering period plus

8   quarter of its duration); ‡ obtained from COMPADRE Plant Matrix Database; referred life history: A = annual, B = biennial, P = perennial; Origin: CZ = Czech Republic, DE

9   = Germany, FR = France, NO = Norway, NL = Netherlands, SE = Sweden.

A1. Demographic matrices of species under study used for wavespeed modelling and
calculation of simple proxy measures related to demography.

If more than one matrix was available for a species, we used those matrices that enabled us to
construct a single mean matrix with λ > 1 (shown below) by simple taking the mean of each
transition. The transitions involving seed dispersal are given in **bold**.

To calculate seedling production and survival, all individuals produced by flowering
individuals to the next year were considered as seedlings. When more than one stage was used
to derive the production and survival of seedlings, we calculated weighted mean of given
values based on stable stage distribution of population.

Agrimonia eupatoria

	Seedling	Juvenile	Vegetative	Reproductive
Seedling	0.0000	0.0000	0.0000	**0.2133**
Juvenile	0.6129	0.5130	0.0000	0.0000
Vegetative	0.0000	0.1829	0.6778	0.1447
Reproductive	0.0000	0.0000	0.2631	0.8530

Anthericum ramosum

	Seed	Seedling	Small vegetative clon	Large vegetative clon	Small vegetative	Large vegetative	Flowering	Flowering clon
Seed	0.3850	0.0000	0.0000	0.0000	0.0000	0.0000	**5.7997**	**5.7997**
Seedling	0.2115	0.0000	0.0000	0.0000	0.0000	0.0000	**1.4288**	**1.4288**
Small vegetative clon	0.0000	0.0000	0.1492	0.1492	0.1492	0.1492	0.1492	0.1492
Large vegetative clon	0.0000	0.0000	0.0000	0.0133	0.0000	0.0133	0.0133	0.0133
Small vegegetative	0.0000	0.7233	0.5961	0.1686	0.5961	0.1686	0.1237	0.1237
Large vegetative	0.0000	0.0000	0.1883	0.3408	0.1883	0.3408	0.3657	0.3657
Flowering	0.0000	0.0000	0.0580	0.4067	0.0580	0.4067	0.4160	0.4160
Flowering clon	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0092	0.0092

3

26   *Anthyllis vulneraria*

	Seeds	Seedlings	Vegetatives	Flowering plants
Seeds	0.1000	0.0000	0.0000	**25.8250**
Seedlings	0.1750	0.0000	0.0000	**6.1750**
Vegetatives	0.0000	0.1075	0.2045	0.0000
Flowering plants	0.0000	0.1495	0.3740	0.1750

27

28

29   *Aster amellus*

	Seedling	Vegetative	Vegetative clon	Reproductive	Reproductive clon
Seedling	0.2256	0.0000	0.0000	**0.1655**	**0.1655**
Vegetative	0.3692	0.8133	0.8133	0.6820	0.6820
Vegetative clon	0.0000	0.0568	0.0568	0.0574	0.0574
Reproductive	0.0128	0.1251	0.1251	0.2192	0.2192
Reproductive clon	0.0000	0.0013	0.0013	0.0027	0.0027

30

31

32   *Aster linosyris*

	Seedling	Small vegetative	Large vegetative	Flowering
Seedling	0.0000	0.0000	0.0000	**0.8287**
Small vegetative	0.1492	0.6190	0.2640	0.2769
Large vegetative	0.0000	0.3586	0.6965	0.6602
Flowering	0.0000	0.0567	0.1840	0.5132

33

34

35   *Carlina vulgaris*

	Small vegetative	Large vegetative	Flowering
Small vegetative	0.5517	0.0000	**2.1333**
Large vegetative	0.3017	0.3080	0.0000
Flowering	0.0000	0.6550	0.0000

36

37

38   *Cirsium acaule*

	Seedling	Vegetative	Vegetative clon	Reproductive
Seedling	0.3599	0.0206	0.0206	**0.5314**
Vegetative	0.3844	0.9012	0.9012	0.8513
Vegetative clon	0.0000	0.0519	0.0519	0.0119
Reproductive	0.0156	0.0302	0.0302	0.1409

39

40

41   *Cirsium pannonicum*

	Seedling	Vegetative	Vegetative clon	Reproductive
Seedling	0.4069	0.0283	0.0283	**0.7840**
Vegetative	0.1158	0.8434	0.8434	0.7691
Vegetative clon	0.0000	0.0361	0.0361	0.0258
Reproductive	0.0417	0.1010	0.1010	0.2031

42

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44   *Falcaria vulgaris*

	Small vegetative	Large vegetative	Flowering
Small vegetative	0.4938	0.2562	**4.2073**
Large vegetative	0.2744	0.5946	0.1315
Flowering	0.0367	0.0546	0.5985

45

46

47   *Linum catharticum*

	Seed	Vegetative	Flowering 1st year	Flowering 2nd year
Seed	0.0000	0.0000	**17.9226**	**116.4969**
Vegetative	0.0043	0.0000	0.0774	0.5031
Flowering 1st year	0.1130	0.0000	**2.0253**	**13.1641**
Flowering 2nd year	0.0000	0.5570	0.0000	0.0000

48

49

50   *Linum flavum*

	Seedlings	Vegetative	Flowering
Seedlings	0.0589	0.0000	**111.7778**
Vegetative	0.1633	0.0278	0.0000
Flowering	0.0000	0.7189	0.8744

51

52

53 *Linum tenuifolium*

	Seedlings	Vegetative	Flowering
Seedlings	0.1500	0.0000	**5.1200**
Vegetative	0.2278	0.3978	0.1456
Flowering	0.0856	0.2867	0.5867

54

55

56 *Plantago media*

	Seedling	Juvenil	Vegetative small	Vegetative large	Flowering
Seedling	0.0000	0.0000	0.0000	0.0000	**0.1860**
Juvenil	0.2000	0.1430	0.0000	0.0000	0.0000
Vegetative small	0.0000	0.2860	0.4670	0.1000	0.0230
Vegetative large	0.0000	0.0000	0.4670	0.5000	0.0930
Flowering	0.0000	0.0000	0.0000	0.4000	0.8840

57

58

59 *Primula veris*

	Seed	Seedling	Small vegetative	Intermediate vegetative	Large vegetative	Flowering
Seed	0.1010	0.0000	0.0000	0.0000	0.0000	**10.9470**
Seedling	0.1345	0.0000	0.0000	0.0000	0.0000	**14.5770**
Small vegetative	0.0000	0.5862	0.6667	0.0000	0.0000	0.0000
Intermediate vegetative	0.0000	0.0000	0.0370	0.5200	0.0250	0.0101
Large vegetative	0.0000	0.0000	0.0000	0.2800	0.5333	0.5657
Flowering	0.0000	0.0000	0.0000	0.0400	0.4083	0.4444

60

61

62   *Scorzonera hispanica*

	Small vegetative	Large vegetative	Flowering
Small vegetative	0.8389	0.0118	**1.6234**
Large vegetative	0.0313	0.7478	0.3098
Flowering	0.0000	0.2243	0.6611

63

64

65   *Trifolium montanum*

	Juvenile	Small vegetative	Large vegetative	Flowering
Juvenile	0.3230	0.0000	0.0000	**1.2750**
Small vegetative	0.1440	0.4420	0.0830	**0.1720**
Large vegetative	0.0180	0.3510	0.5410	0.3910
Flowering	0.0000	0.0580	0.3090	0.5600

66

67

68   **A2**. Modelling wind dispersal.

69   The WALD is a mechanistic model, using wind speed and characteristics of the vegetation

70   and species (seed release height and terminal velocity) to derive a probability density function

71   (PDF) of dispersal distances (i.e. dispersal kernel). The PDF of the WALD model is

72   $$p(r,u) = \left(\frac{\lambda'(u)}{2\pi r^3}\right)^{\frac{1}{2}} \exp\left[-\frac{\lambda'(u)(r-\mu'(u))^2}{2\mu'^2(u)r}\right],$$

73   where r is distance, $\lambda'(u)$ is the scale parameter and $\mu'(u)$ is the location parameter of the

74   function. The latter two parameters are dependent on wind speed (u) and related to

75   measurable species' parameters as follows:

76   $$\mu'(u) = \frac{HU(u)}{F},$$

77   $$\lambda'(u) = \left(\frac{H}{\sigma(u)}\right)^2.$$

78   The required parameters are therefore: seed release height H, mean wind speed at the height

79   of seed release $U(u)$, seed terminal velocity F and turbulent flow parameter $\sigma(u)$. As wind

80   speeds were measured at 10 m height and had to be corrected to give the wind speed at the

81   height of seed release, we derived $U(u)$ by integrating wind speed over a logarithmic wind

82   profile see Bullock et al. (2012),

83   $$U(u) = \frac{1}{H}\int_l^H \frac{U*(u)}{K}\log\left(\frac{z-d}{z_0}\right)dz,$$

84   where $U*(u)$ is the friction velocity, K is the von Karman constant (0.4), z is the height above

85   ground and d and z_0 are surface roughness parameters. The lower limit of the integral is $l = d$

86   $+ z_0$. As the species disperse over short herbaceous vegetation (constant for all species and set

87   as $h = 0.05$ m), the surface roughness parameters are related to h by $d \approx 0.7h$ and $z_0 \approx 0.1h$. The

88   friction velocity $U*(u)$ and turbulent flow parameter $\sigma(u)$ were calculated from the equations

89   A2 and A4 in Skarpaas and Shea (2007), respectively, which are both functions of the

90   measured wind speed and vegetation height.

91

92 **Table A2**. Spearman's rank correlation coefficients of species' characteristics under study.

93 Significant correlations (P < 0.05) are highlighted in **bold**.

		Dispersal				Demography		
		Ddist	Pheight	Vterm	Windsp	λ	Sprod	Ssurv
Dispersal	Pheight	**0.518**						
	Vterm	**−0.626**	0.191					
	Windsp	0.033	0.188	0.094				
Demography	λ	−0.312	−0.097	0.174	0.438			
	Sprod	−0.326	−0.150	0.274	**0.623**	**0.874**		
	Ssurv	**0.568**	0.385	−0.079	−0.056	−0.382	−0.171	
	Fsurv	−0.204	0.021	0.316	0.029	**−0.531**	−0.469	−0.083

94 Note: Ddist = Dispersal distance; Pheight = Plant height; Vterm = Terminal velocity; Windsp = Wind speed; λ =

95 Population growth rate; Sprod = Seedling production; Ssurv = Survival of seedlings; Fsurv = Survival of

96 flowering individuals.

97

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