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New Phytologist

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<https://doi.org/10.1111/j.1469-8137.2009.02948.x>

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Darwin's wind hypothesis: does it work for plant dispersal in fragmented habitats?

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Summary

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Received: 15 May 2009

Accepted: 4 June 2009

New Phytologist (2009) **183**: 667–677

doi: 10.1111/j.1469-8137.2009.02948.x

Key words: common garden, evolution of dispersal, fragmentation, latitudinal gradient, leading edge hypothesis, phenotypic variation.

- Using the wind-dispersed plant *Mycelis muralis*, we examined how landscape fragmentation affects variation in seed traits contributing to dispersal.
- Inverse terminal velocity (V_t^{-1}) of field-collected achenes was used as a proxy for individual seed dispersal ability. We related this measure to different metrics of landscape connectivity, at two spatial scales: in a detailed analysis of eight landscapes in Spain and along a latitudinal gradient using 29 landscapes across three European regions.
- In the highly patchy Spanish landscapes, seed V_t^{-1} increased significantly with increasing connectivity. A common garden experiment suggested that differences in V_t^{-1} may be in part genetically based. The V_t^{-1} was also found to increase with landscape occupancy, a coarser measure of connectivity, on a much broader (European) scale. Finally, V_t^{-1} was found to increase along a south–north latitudinal gradient.
- Our results for *M. muralis* are consistent with 'Darwin's wind dispersal hypothesis' that high cost of dispersal may select for lower dispersal ability in fragmented landscapes, as well as with the 'leading edge hypothesis' that most recently colonized populations harbour more dispersive phenotypes.

Introduction

A major threat to biodiversity is the ongoing fragmentation of habitats (Fahrig, 2003). Dispersal ability is critical to the demographic and evolutionary persistence of a species in fragmented landscapes as it allows exchange of individuals and genes among fragments, the recolonization of empty habitat, and even local adaptation (Alleaume-Benharira *et al.*, 2006; Bridle *et al.*, 2009). Seed dispersal distances vary with many environmental factors (Nathan *et al.*, 2008), as well as with plant traits for which there is genetic variation both between and within populations (Venable & Burquez, 1989;

Imbert, 2001; Donohue *et al.*, 2005; Riba *et al.*, 2005). Traits influencing seed dispersal ability can evolve quickly in response to change in selection pressures (Cody & Overton, 1996; Cheptou *et al.*, 2008). While data accumulates on the ecological consequences of fragmentation, little is understood about the evolutionary processes accompanying fragmentation. Theoretical models predict that evolution of dispersal traits in a changing landscape could rescue a metapopulation from extinction (evolutionary rescue, Heino & Hanski, 2001) or, by contrast, accelerate its collapse (evolutionary suicide, see the general discussion in Ferrière *et al.*, 2004). Within this context, concerns have been raised that increasing landscape fragmentation may select for genotypes with lower dispersal ability, which may aggravate rather than mitigate the consequences of fragmentation.

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The idea that isolation might select for genotypes with poor dispersal ability dates back to Darwin's wind hypothesis about the loss of wings in insects and birds following colonization and establishment on islands (Darwin, 1859, p. 135). His idea was that wings would allow wind to blow organisms into unfavourable water masses, and thus the loss of wings would be favoured by natural selection on small, isolated islands (but see Denno *et al.*, 2001 for alternative explanations). In plants, dispersal structures such as a pappus play the same role as wings in insects and Darwin's wind hypothesis has been invoked to explain the reduced dispersal ability of seeds in plants on small isolated islands compared with populations on the mainland (Cody & Overton, 1996; Fresnillo & Ehlers, 2008). Since fragmented habitats can be regarded as 'islands' of favourable habitat surrounded by an unsuitable matrix, it is tempting to quantify the connectedness of habitat fragments and use this to test the hypothesis that fragmentation has caused evolutionary changes in particular seed traits affecting dispersal ability. In other words, can Darwin's wind hypothesis help us to understand the evolution of dispersal in fragmented landscapes?

However, landscape fragmentation is a complex process, varying in the number of habitat fragments in the landscape, their size and quality, the distance separating them, and the nature of the suboptimal habitat between fragments (Fahrig, 2003; Ewers & Didham, 2006). Some species in some landscapes have had patchy distributions for long periods, while for others fragmentation is a recent and ongoing process, probably with distinct evolutionary consequences. Understanding the consequences of habitat fragmentation for the evolution of dispersal requires taking all these dimensions into account. Predictions of the effect of fragmentation on dispersal evolution are then more complex than the simple reduction in dispersal traits predicted by Darwin's wind hypothesis and are likely to vary with the scale of the analysis, the pattern of fragmentation and its extent.

At the landscape scale, fragmentation (greater distances among fragments) may increase the mortality associated with dispersal (for a quantification of this cost see Cheptou *et al.*, 2008), and theory predicts that traits favouring dispersal are then selected against, consistent with Darwin's wind hypothesis (Comins *et al.*, 1980; Olivieri *et al.*, 1995; Gandon & Michalakis, 1999). However, fragmentation also results in higher genetic similarity among neighbouring plants and faster turnover of populations because of smaller population sizes and stronger isolation, which are expected to select for increased dispersal ability of seeds (see the models by Comins *et al.*, 1980; Frank, 1986; Gandon & Michalakis, 1999). Complex patterns of dispersal evolution may then emerge when the different facets of fragmentation are jointly simulated (Heino & Hanski, 2001). Theoretical models have also shown how variation in the risks associated with dispersal would affect the spatial distribution of dispersing genotypes within a given landscape (Travis & Dytham, 1999; Hanski *et al.*, 2004; Gros

et al., 2006). Predictions arising from these models indicate that isolated habitat fragments contain more dispersive genotypes than well-connected fragments when they have just been recolonized, while the reverse trend holds for fragments occupied for a longer time (Hanski *et al.*, 2004; for a theoretical description of this 'metapopulation effect' see also Olivieri *et al.*, 1995; Olivieri & Gouyon, 1997).

In plants, studies investigating the evolution of dispersal ability across landscapes with different connectivity are rare. This might arise from inherent difficulties in defining, *a priori*, patches of suitable and unsuitable habitat for many plant species (Ouborg & Eriksson, 2004). Recent work by Cheptou *et al.* (2008) on the heteromorphic plant *Crepis sancta* (Asteraceae) used a highly fragmented urban landscape, with clearly unsuitable habitat between patches of plants, to overcome this difficulty. They found that populations of *C. sancta* have evolved to produce fewer dispersed seeds in an urban landscape compared with continuous populations in a nearby rural area. In agreement with the 'metapopulation effect' described earlier, which occurs within landscapes, Cody & Overton (1996) found that seed dispersal ability in *Mycelis muralis* and *Hypochoeris radicata* (Asteraceae) was greater on recently colonized islands than on the mainland, but decreased below the mainland level with time since colonization (for changes in seed dispersal ability with population age see also Olivieri & Gouyon, 1985; Peroni, 1994). In recently fragmented landscapes, seed dispersal potential was found to increase, decrease or be unaffected by the local population size in isolated remnant populations of several Asteraceae species (Soons & Heil, 2002; Mix *et al.*, 2006), although in these cases, resource allocation as a result of inbreeding effects, rather than rapid selection of new dispersal strategies, was the likely cause.

A final feature of plant populations that must be considered in the study of the relationship between habitat fragmentation and the evolution of dispersal ability is their recent history of expansion following the last glaciation. Landscapes colonized more recently have been found to harbour plants with more dispersive phenotypes (Cwynar & MacDonald, 1987; Darling *et al.*, 2008), which is in agreement with theoretical predictions about the evolution of dispersal ability in expanding species (Travis & Dytham, 2002; Dytham, 2009). Metapopulations inhabiting landscapes at the leading edge of a species range may not be at equilibrium, and their genetic diversity and functioning can be very different from that in landscapes occupied for longer evolutionary times (Parisod & Bonvin, 2008; Parisod & Christin, 2008; Purves, 2009). Sorting of dispersal genotypes with landscape connectivity may therefore differ in regions with different post-glacial histories.

In the present paper, we used the wind-dispersed plant *M. muralis* to examine the relationship between the dispersal ability of seeds and landscape fragmentation. Our aim is not to quantify the effect of fragmentation on effective dispersal between fragments, but instead to assess whether fragmentation might have caused evolutionary changes in seed traits affecting

dispersal ability. We use a correlative approach as a first attempt to address this question. We conducted our analysis at two spatial scales. First, we studied eight landscapes in detail in Spain, at the southern edge of the species distribution, where *M. muralis* is the most patchily distributed. Here, we related the inverse terminal velocity (V_t^{-1}), a surrogate for individual seed dispersal ability, of achenes sampled in the field to measures of landscape connectivity based on the sizes of patches and distances between them. We tested whether the observed differences in V_t^{-1} might be at least partly genetically based by growing maternal families from two of the Spanish populations in a common garden experiment with experimental conditions as close as possible to natural conditions. Second, at a broader scale, we studied 29 landscapes within three geographical regions at the European scale (northern, western central and southern Europe). Using a coarser measure of connectivity (landscape occupancy), we examined the relationship between V_t^{-1} of achenes sampled in the field and landscape occupancy at the European scale. We also examined how V_t^{-1} varied across regions for a given level of landscape occupancy. *M. muralis* has been part of the vegetation for different lengths of time after post-glacial migration in the different regions. Because the northern region is the most recently colonized, we expect that seed dispersal ability should be greater in this region than in the two others, regardless of the degree of landscape fragmentation.

Materials and Methods

Study species, sampling sites and habitat characteristics

The species *M. muralis* (L.) Dumort. (Asteraceae) is a diploid and predominantly selfing plant (Chauvet *et al.*, 2004) that occurs throughout most of Europe, where it is native. Although the species has been reported as annual or biennial in North America (Cody & Overton, 1996), it has only been described as perennial in Europe (Sell, 1993; Clabby & Osborne, 1999). The species is usually found on calcareous or base-rich soils in moist and open habitats, such as forest gaps and margins, and rock outcrops. Habitat fragmentation in *M. muralis* is therefore not necessarily associated with more open landscapes but, instead, in the southern part of its range, with increased forest cover. Plants flower and set seed for an extended period in the summer (see details in the Supporting Information and Fig. S1). Each flower-head usually produces five achenes, and a dispersal unit (hereafter called seed) consists of an achene with a pappus. Seeds are readily blown by gusts of wind a few minutes after flower-heads open, and often some pappus hairs readily detach once the seed falls to the ground (pers. obs.). The species is not known to form permanent seed banks (Clabby & Osborne, 1999) and seed viability drops to 1.5% after 2 yr (M. Riba *et al.*, unpublished). Additional information on the species, its distribution and its habitat can be found in Clabby & Osborne (1999) and Chauvet *et al.* (2004).

During the year 2000, 29 localities (hereafter called landscapes) were selected in three areas along the latitudinal distribution area of *M. muralis* in Europe: 12 landscapes in the south (eight in north-eastern Spain and four in southern France), nine in western central Europe (the Netherlands) and eight in the north (Sweden). Landscapes were selected so as to cover the whole range of geographical abundances in each region, based on the known distribution from the regional floras. We define a landscape as a local area within a 1500 m radius around a 'focal' cluster (patch) of *M. muralis* plants. Focal patches corresponded to the most conspicuous cluster of plants found under first inspection. Circles of 1500 m radius were chosen as landscape areas because previous studies based on microsatellite markers indicated strong genetic differentiation among patches separated by a few kilometres (Chauvet *et al.*, 2004), suggesting that most gene flow occurs over this scale.

Landscapes in Spain and France lie in the southern limit of the current distribution in Europe, and they probably represent relict populations from a wider distribution during the last glaciation (Chauvet *et al.*, 2004). By contrast, landscapes in Sweden lie in the northern limit of the species range and are located along the coast and on islands in the Gulf of Bothnia. This area experiences an isostatic rebound of 6.5 mm yr⁻¹, which potentially creates new suitable habitat (Ericson & Wallentinus, 1979), and thus populations are expected to be recent postglacial recolonizations (Chauvet *et al.*, 2004). Altitudinal data from topographic maps suggest that the maximum population age would be 700 yr, and in most cases much younger. Within the Netherlands, the species is usually found in anthropogenically disturbed places, such as urban areas. Distances among regions, the names of each landscape, their locations and details of habitat type are given in the Supporting Information (Fig. S2 and Table S1).

Plant sampling

Between 2000 and 2002, a variable number of plants (Table S1) and seeds per plant were sampled (2–30, 4–25, 10 and 9–10 seeds per plant for Spain, France, the Netherlands and Sweden, respectively). Each individual seed was placed in an Eppendorf tube for later measurement (see below). Depending on the availability of ripe seeds at the time of collection, achenes were sampled either in the focal patch only or in several patches in the landscape.

The nature of *M. muralis* populations in Spain, forming few, clearly isolated clusters of plants, allowed a more detailed analysis of the relationship between landscape connectivity and seed dispersal traits. We therefore first present the methods used when analysing this relationship at the scale of the eight Spanish landscapes. We then describe how these methods were modified to document a similar relationship at the broader European scale using all 29 landscapes.

Comparison among Spanish landscapes: estimates of connectivity

Within each landscape we intensively searched and accurately mapped focal and all other plant patches in the landscape (i.e. groups of plants separated by at least 25 m). For each patch we also estimated its size (m²) and counted all flowering plants. Mapping was performed using a GPS device (Garmin eTrex Legend, position accuracy 3–5 m), supplemented by a compass and measuring tape for those patches too closely situated to be resolved by GPS. These data allowed us to calculate two connectivity measures that capture the degree of isolation in terms of dispersal and colonization events (for a theoretical explanation see Moilanen & Nieminen, 2002): a nearest-neighbour index of isolation (I_i) and a connectivity measure (S_i) based on the Incidence Function Model (IFM; Hanski, 1994):

$$I_i = \frac{d_{\text{NN}}}{A_i^c(1 + A_{\text{NN}}^b)} \quad S_i = A_i \left(1 + \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^b \right)$$

A_i and A_{NN} are the number of flowering plants in the focal patch and its nearest neighbour ‘contributing’ patch (i.e. potentially exchanging propagules with the focal patch), respectively; d_{NN} is the distance from the focal patch to the nearest neighbour patch; A_j is the number of plants in the contributing patch j ; d_{ij} the distance between the focal patch i and each contributing patch j . Distances are measured in metres. The expressions are slightly modified from those given by Moilanen & Nieminen (2002), to avoid infinite values that arise when log-transformed measures of isolation or connectivity are used for surveyed areas containing only a single patch. For landscapes with no observed contributing patches, d_{NN} was set to 1500 m. Parameters b and c were used for scaling emigration and immigration as a function of patch size, respectively, while α is a parameter for scaling the effect of distance on dispersal. In our case, all three parameters are unknown. We used a value of 1 for both b and c , which means that emigration and immigration depend simply on the number of plants in patches, as might be expected for the passive diffusion process of dispersal in plants. We used three different values for α , corresponding to contrasting extreme scenarios. With $\alpha = 0$, all patches within 1500 m are assumed to contribute equally to the pool of potential immigrants (no isolation by distance). With $\alpha = 10^{-2}$, patches further than 500 m are unlikely to contribute migrants to the focal patch. With $\alpha = 10^{-3}$ (an intermediate case), contribution of patches declines with distance but is negligible only above 1000 m.

Finally, for comparison with other European landscapes (described later), we computed a coarser measure of the spatial distribution of plants, landscape occupancy (LO) as the percentage of the landscape area (circle of 1500 m radius, i.e. 7.07 km²) occupied by plant patches. This latter measure ignores the distances between patches of plants.

Comparison among Spanish landscapes: measurements of seed wind-dispersal potential

Together with plant height, one of the main plant-controlled components of mechanistic models to predict seed dispersal in anemochorous plants is the speed of descent: terminal velocity (V_t) or its inverse (V_t^{-1}) (Sheldon & Burrows, 1973; Okubo & Levin, 1989; for a recent review see Kuparinen, 2006). Terminal velocity V_t was measured from drop time. Although drop time depends on an acceleration phase and a constant rate of fall, terminal velocity in most achene-pappus units is quickly reached (Sheldon & Burrows, 1973). Drop times were measured in a Perspex tube (diameter 30 cm), cleaned before measurement with an antistatic agent, by measuring the times that seeds took to descend through a vertical distance of 1.78 m with a stop watch. Drop time for each seed was estimated as an average of two trials. Only measurements from seeds with widely-deployed pappi, that remained completely undamaged over repeated trials, were included in the data set. Paired analyses comparing the same seeds between the first and second trials did not show any significant effect (repeated measures ANOVA: $P = 0.845$, $n = 44$). The data consist of the means of the repeated trial for each seed.

The limited availability of ripe seeds at the time of collection did not allow sampling of a sufficient number of seeds with either completely undamaged pappi (all pappus hairs intact) or with the pappi widely deployed after flower-head opening to obtain an adequate number of measures of V_t . Instead, V_t was estimated from seed morphological traits. For every seed we measured pappus length (mm), achene length (mm), maximum achene width (mm) and achene weight (milligrams, precision = 0.01 mg). Pappus length, achene width and achene length were measured under a binocular microscope ($\times 60$ magnification) (total number of seeds measured was 2802). Using a subsample of 44 seeds from five Spanish landscapes (5–15 seeds per landscape) for which V_t was measured from drop time, we regressed V_t on a linear combination of seed morphological traits (stepwise regression, Proc REG, SAS, 2002). Seed V_t was then predicted for every seed from the linear combination of their morphological traits using the previous regression.

Comparison among Spanish landscapes: common garden experiment

Seeds from two focal patches from the Spanish landscapes differing in seed terminal velocity in natural conditions (populations COL and BAL, see Table 1 and Fig. S2), were grown in a common garden at the experimental fields of the Autonomous University of Barcelona (Bellaterra, Spain). Seeds from 10 (COL) and 26 (BAL) maternal plants (full-sib families) were collected in summer 2002. Ten seeds per family were germinated in autumn 2003 and grown in a fully randomized design. Experimental conditions were kept as

Table 1 Characteristics of focal patches and landscapes in the Spanish locations selected

Landscape	Focal patch size (m ²)	Number of flowering plants in focal patch	Distance to the nearest contributing patch (m)	Number of patches in landscape	Mean nearest-neighbour distance among patches (m)	Isolation index (I)	IFM-based connectivity (S) α = 10 ⁻²	Number of plants sampled
BAL	5520	399	25.5	48	57.2	0.0058	20 376.03	54
BAS	6	5	1500.0	1	1500.0	300.0000	5.00	2
BUR	171	33	1500.0	1	1500.0	45.4545	33.00	12
CAR	315	25	80.0	3	53.9	0.2000	243.08	20
CFT	3705	2030	25.0	26	120.9	0.0001	3 139 794.24	25
COL	63	24	129.8	14	141.2	2.7049	110.01	23
FOU	283	40	27.6	19	125.1	0.3453	189.25	17
VID	50	63	37.5	5	663.1	0.0165	1578.64	16

Details on sampling procedures and estimates of isolation (I) and connectivity (S) indices are given in the text. IFM, Incidence Function Model; BAS, Basiet; BAL, Balma; BUR, Bargar; CAR, Cargol; CFT, Castellfollit; COL, Collformic; FOU, Fou; VID, Vidalbar; see the Supporting Information for further details on location and habitat characteristics.

close as possible to those of the natural habitats. Plants were grown in an open glasshouse under shading and watered as needed to prevent mortality. Most of the plants that survived the seedling stage flowered in early summer 2004 and seeds were collected from 10 (COL) and 20 (BAL) families (1–9 offspring per family, mean 3.2). Individual seed traits were measured and V_t^{-1} was estimated on 10 seeds per plant using the same predictive relationship as for seeds from natural populations (see above).

Comparison among Spanish landscapes: data analyses

The potential for dispersal ability of individual seeds is expressed by the inverse of its predicted terminal velocity (V_t^{-1}). The variability in dispersal ability measured by V_t^{-1} among landscapes in natural conditions was analysed using one-way analysis of variance. The variability in V_t^{-1} between populations and among families within population in the common garden experiment was assessed using ANOVA (Proc GLM in SAS, 2002), declaring Population as a fixed factor and Family as a random factor nested within Population. The relationships between seed dispersal potential and landscape connectivity indices were tested through Pearson product moment correlations, using data on predicted V_t^{-1} obtained from plants in focal patches. All the connectivity metrics (I_i , S_i and LO) used for these tests were log-transformed to achieve linearity. Additional simple relationships between pairs of variables were assessed with Pearson's (when linear) or Spearman's rank correlations (linearity not met). Where means are quoted, their associated 95% confidence intervals (± 1.96 SE) are given throughout unless otherwise stated.

Comparisons across European landscapes

In other European sites, the spatial distribution of *M. muralis* formed a complex matrix of numerous patches, with many singletons (especially in the Swedish sites), which prevented a clear distinction between focal and contributing patches. We thus recorded the numbers and areas of patches, and numbers of plants per patch within a circle of 1500 m radius. Therefore, when comparing the within-landscape connectivity and seed dispersal potential at the European scale, only measures of landscape occupancy (LO) were used as previously described for Spanish landscapes.

In France, seed terminal velocity was predicted from seed morphological measurements as was done in Spain (total number of seeds measured was 1404). For Dutch and Swedish landscapes, the availability of plants and seeds allowed V_t to be measured directly for every individual seed from drop time. Drop time measurements were carried out as described earlier except that a vertical distance of 2 m was used and data consist of the average of three drop trials for each seed (total number of seeds measured: Sweden $n = 1790$; Netherlands $n = 2250$). We checked that the difference in tube height used in different

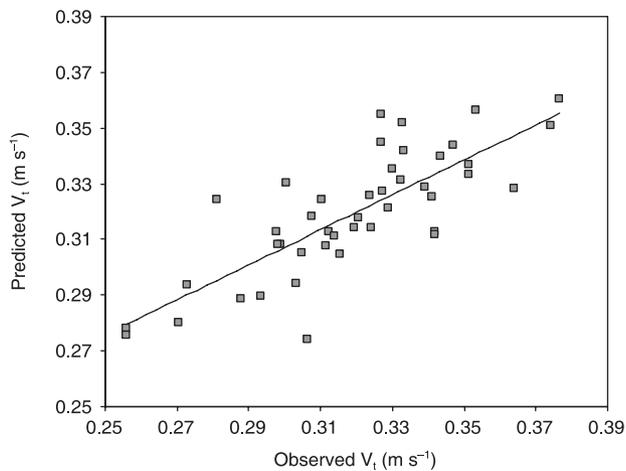


Fig. 1 Relationship between predicted, based on morphological traits, and observed terminal velocity (V_t) of *Mycelis muralis* seeds. $r^2 = 0.63$; slopes (\pm SE): achene length = $0.039 (\pm 0.009)$, maximum achene width = $0.094 (\pm 0.041)$, pappus length = $-0.036 (\pm 0.008)$, achene weight = $0.119 (\pm 0.059)$.

countries produced negligible bias in the estimation of terminal velocity in comparison with the differences between landscapes.

Differences among regions in LO were analysed using one-way analysis of variance. To analyse the relationship between LO and seed dispersal ability (V_t^{-1}) across European regions we used the following analysis of covariance model: LO + Region + LO \times Region. The analysis was performed on V_t^{-1} values (either predicted or measured) for all plants sampled in each landscape. Pairwise tests for differences among regions or landscapes within regions after ANOVA or ANCOVA were conducted on least-squares means using the LSMEANS option of Proc GLM in SAS (SAS, 2002), with P -values adjusted for multiple comparisons (Tukey–Kramer method).

Results

Best predictor of terminal velocity for southern landscapes

The step-wise procedure selected all measured morphological traits as potentially explanatory variables. Achene length and pappus length were highly significant ($P < 0.001$), maximum achene width was significant ($P = 0.028$) and achene weight was marginally significant ($P = 0.052$). The linear combination of these variables accounted for 63% of the variance in terminal velocity (overall model: $P < 0.001$). Including interactions between predictor variables or assuming nonlinear relationships between predictors and the response variable did not improve the fit. The resulting best predictor equation is (Fig. 1):

$$V_t = 0.248 + 0.039 \times \text{achene length} + 0.094 \times \text{achene width} + 0.119 \times \text{achene weight} - 0.036 \times \text{pappus length}.$$

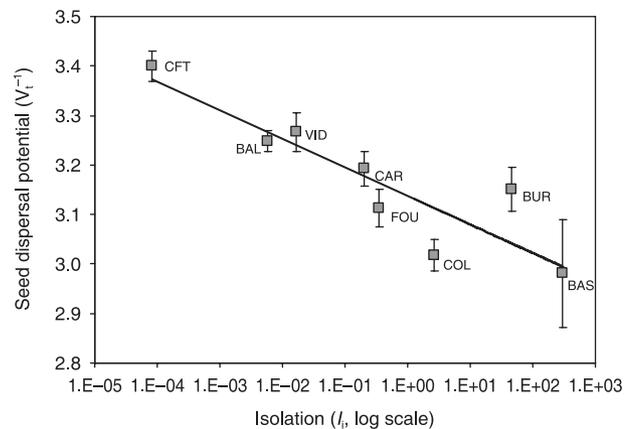


Fig. 2 Seed dispersal potential ($V_t^{-1} \pm$ SE) and isolation (I_i index) for Spanish focal patches of *Mycelis muralis* plants (see the Supporting Information, Fig. S2, for locations of the patches).

Individual seed dispersal potential and connectivity in Spain

Strong associations were found among most of the variables that could be used to assess the degree of landscape connectivity (Table 1). In particular, log-transformed measures of landscape isolation (I_i) and connectivity (S_i) were highly correlated (Pearson: r between -0.94 and -0.96 and $P < 0.001$ for all connectivity α -values tested), and both captured the essential features related to habitat fragmentation. Thus, for example, the index of landscape isolation (I_i) was significantly and negatively correlated with LO (Spearman: $r = -0.74$; $P = 0.037$) and the number of patches in the landscape (Spearman: $r = -0.78$; $P < 0.01$), and positively, though marginally, significantly associated with the mean nearest-neighbour distance between landscape patches (Spearman: $r = 0.71$ $P = 0.05$). These observations indicate that the gradient of connectivity included in the landscapes sampled in Spain show some of the basic and common features usually associated with long-term outcomes arising from the process of habitat fragmentation (i.e. decreasing number of fragments and increasing isolation among them).

The analysis of the phenotypic variability in V_t^{-1} conducted for focal patches in Spanish landscapes revealed strong differences among landscapes (ANOVA: $F_{7,161} = 13.0$, $P < 0.0001$). Seed dispersal potential (V_t^{-1}) decreased significantly with log-transformed isolation (I_i ; Pearson $r = -0.90$; $P < 0.01$; Fig. 2) and increased with log-transformed connectivity. Connectivity measures performed similarly to the simple isolation index in explaining variation in V_t^{-1} only when we assumed short dispersal distances ($\alpha = 10^{-2}$, Pearson $r = 0.90$; $P < 0.01$). The V_t^{-1} value was also positive and significantly correlated with log-focal patch size (Pearson $r = 0.76$; $P < 0.01$) and the log-transformed number of flowering plants (Pearson $r = 0.89$; $P < 0.01$). These relationships were also significant after removing the data from the BAS population,

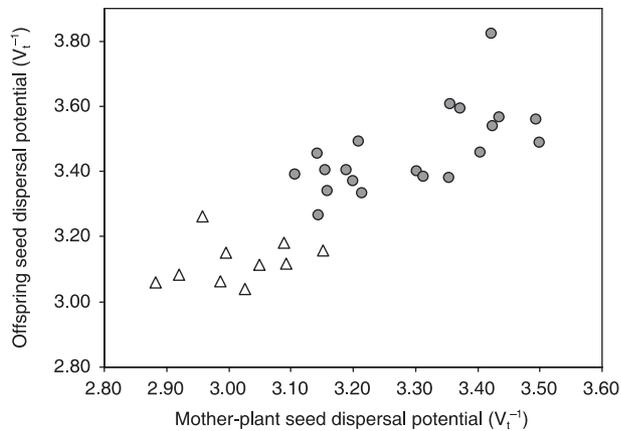


Fig. 3 Parent (natural conditions)–offspring (common garden) relationship for seed dispersal potential (V_t^{-1} , in s m^{-1}) of *Mycelis muralis* plants. Populations: circles, BAL; triangles, COL.

which was estimated from a limited number of available plants (Table 1).

Genetic basis of wind-dispersal potential in Spanish landscapes

The results obtained from the common garden experiment suggest that the phenotypic differences in V_t^{-1} found under natural conditions among Spanish landscapes might have a genetic basis. We observed significant differences in V_t^{-1} values between focal patches from different landscapes (Fig. 3, ANOVA: $F_{1,34} = 70.4$, $P < 0.001$), as well as significant variation among families within populations (ANOVA: $F_{28,67} = 2.7$, $P < 0.001$). Mean values of V_t^{-1} (in s m^{-1}) for BAL were higher than those for COL, both in the field (BAL = 3.248 ± 0.041 ; COL = 3.018 ± 0.063) and the common garden experiment (BAL = 3.463 ± 0.033 ; COL = 3.123 ± 0.039). We observed no significant differences among families within COL (ANOVA: $F_{9,31} = 1.1$, $P = 0.419$), but significant differences within BAL (ANOVA: $F_{19,36} = 3.3$, $P < 0.01$). Parent–offspring regression in this latter case was also significant (Slope = 0.63; $r = 0.64$; $P < 0.01$; Fig. 3).

Dispersal ability and landscape occupancy at the European scale

Estimates of LO and the total number of plants were highly correlated (Pearson log-transformed values: $r = 0.84$; $P < 0.001$; $n = 29$). The LO varied among European regions (Fig. 4, ANOVA: $F_{2,26} = 10.7$, $P < 0.001$), and was significantly higher in the northern region ($0.28 \pm 0.08\%$) compared with central ($0.08 \pm 0.08\%$) and southern ($0.04 \pm 0.06\%$) regions ($P < 0.01$ for both pairwise comparisons). Mean LO values in central and southern Europe were not different ($P = 0.418$).

Values of V_t^{-1} at the European scale also varied across landscapes within each region: $2.98\text{--}3.44 \text{ s m}^{-1}$, $3.04\text{--}4.23 \text{ s m}^{-1}$

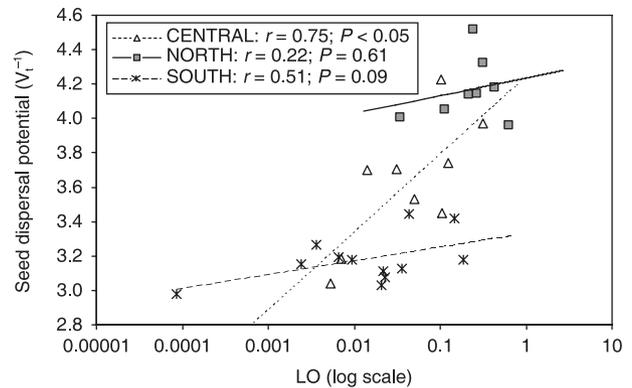


Fig. 4 Variation in seed dispersal potential (V_t^{-1} , in s m^{-1}) in relation to *Mycelis muralis* landscape occupancy (LO) across European landscapes.

and $3.96\text{--}4.52 \text{ s m}^{-1}$ for the southern, central and northern European regions, respectively (Fig. S3). We found significant differences among landscapes within every region in V_t^{-1} (ANOVAs: $F_{11,337} = 15.5$, $P < 0.0001$; $F_{8,261} = 37.0$, $P < 0.0001$; $F_{7,160} = 8.0$, $P < 0.0001$, for southern, central and northern regions, respectively). At the European scale, V_t^{-1} increased with landscape occupancy (log-LO main effect in ANCOVA: $F_{1,23} = 7.7$, $P = 0.010$; Fig. 4). Although the relationship between V_t^{-1} and LO varied according to the region considered (log-LO \times Region in ANCOVA: $F_{2,23} = 4.15$, $P = 0.029$, Fig. 4), this interaction should be interpreted with caution since it is sensitive to removal of data points with extremely poor connectivity in Spain.

For the same level of intermediate LO (0.04%), V_t^{-1} was significantly different among regions, increasing from south to north along the latitudinal gradient (north = $4.09 \pm 0.32 \text{ s m}^{-1}$ > central = $3.61 \pm 0.13 \text{ s m}^{-1}$ > south = $3.22 \pm 0.13 \text{ s m}^{-1}$, $P < 0.001$ for all pairwise comparisons). Furthermore, V_t^{-1} was significantly higher in the north than in the south for all levels of overlapping LO values ($P < 0.001$). When analysing the relationship between landscape occupancy and seed dispersal ability separately in each region, although we found that the relationship between V_t^{-1} and log-LO was positive in all regions, it was not significant for the northern region (Pearson: $r = 0.22$, $P = 0.601$), marginally significant in the south (Pearson: $r = 0.51$, $P = 0.092$) and significant only in central Europe (Pearson: $r = 0.75$; $P = 0.021$). The marginal significance of the relationship between V_t^{-1} and log-LO in the south contrasts with the relationship between V_t^{-1} and isolation described above, which was highly significant. This difference is probably related to the fact that the isolation index integrates both patch densities and distances among patches, whereas landscape occupancy is based on the proportion of area occupied by plants. Hence the isolation index is more likely than the LO to reflect aspects of landscape fragmentation that affect seed dispersal.

Discussion

Our extensive studies of the variation in the seed inverse terminal velocity (V_t^{-1}) of *M. muralis* from 29 landscapes spanning the southern to the northern limits of the species range clearly indicate that the dispersal potential of individual seeds of *M. muralis* increases with landscape occupancy. In the highly fragmented landscapes at the southern limit of the species range, individual seed dispersal potential obtained from predicted V_t^{-1} in focal patches of *M. muralis* significantly increased with the connectivity to other patches of plants. This relationship was robust to the use of various statistical measures for habitat fragmentation and connectivity, that integrate the effects of patch size and distances between them. Our results in a common garden experiment further suggest that part of the observed variability in natural conditions is genetically based. Using a coarser measure of landscape connectivity (LO) we found that V_t^{-1} (observed or predicted depending on the region) increased with LO within the three regions with putatively distinct evolutionary histories (southern, central and northern Europe), the relationship being significant only for (western) central Europe.

The decline in V_t^{-1} with increasing habitat fragmentation in *M. muralis* is consistent with the pattern observed in *C. sancta*, when comparing an urban fragmented landscape with continuous populations within a single region (Cheptou *et al.*, 2008), as well as with the decline in seed dispersal ability on old islands documented by Cody & Overton (1996) in *M. muralis*. Previous studies addressing the consequences of landscape fragmentation on plant dispersal ability have analysed the effect of population size on seed terminal velocity (Soons & Heil, 2002; Mix *et al.*, 2006). The diverging results in these studies (see the Supporting Information, Table S2) have been attributed to the contrasting effects of inbreeding depression on resource allocation patterns. Since *M. muralis* is a selfing species (Chauvet *et al.*, 2004), with probably little inbreeding depression, we expect inbreeding and pollen limitation in small populations to have little effect on seed dispersal traits. The variation for other traits potentially influencing seed dispersal, such as plant height (see Table S2 for an example) was not explored in our study and deserves further investigation. However, preliminary observations on plant size in Spanish populations suggest that, under natural conditions, plants in southern, more fragmented landscapes are smaller, probably because of limiting environmental conditions. Furthermore, there were no significant differences for individual height between the two populations studied in the common garden experiment.

To the best of our knowledge, Mix *et al.* (2006) and Cheptou *et al.* (2008) are the only studies, in the context of fragmentation, in which phenotypic differentiation among populations or landscapes was also studied in a common garden experiment. The experiment we performed on two Spanish populations suggests that in *M. muralis* at least some of the observed pheno-

typic variation has a genetic basis. For these two populations, mean V_t^{-1} estimated from seed traits measured in the field was close to that measured in the common garden and the ranking of the populations with respect to V_t^{-1} was conserved. Similar results were obtained in *Centaurea corymbosa* (Asteraceae) (Riba *et al.*, 2005) and in *Heterosperma pinnatum* (Asteraceae) (Venable & Burquez, 1989) when comparing field and common garden measurements for achene traits. Moreover, in one of our study populations (BAL), seed dispersal ability in the offspring was correlated with that of their parents in the field, suggesting the presence of a genetic component for dispersal within the population. In our common garden experiment, as in previous studies (Riba *et al.*, 2005; Mix *et al.*, 2006; Cheptou *et al.*, 2008), maternal effects may also partly explain parent–offspring resemblance. The lack of evidence for genetic variation in the other population (COL) may be explained by its reduced size, smaller than BAL by an order of magnitude, and its greater degree of isolation. This would be consistent with the theoretical expectation, and widely observed phenomena, of a reduced evolutionary potential in more fragmented habitats, adding to the growing concern about the detrimental consequences of fragmentation.

Limited dispersal potential of individual seeds in the most fragmented landscapes could have far-reaching consequences for the long-term persistence of species and, more generally, population dynamics. In the rare endemic cliff species *C. corymbosa*, it is believed that strong risks associated with dispersal have selected for achenes with poor dispersal ability by wind, resulting in extremely rare events of dispersal between populations and the absence of colonization events despite the existence of suitable habitat in the vicinity of extant populations (Colas *et al.*, 1997; Riba *et al.*, 2005). Using mechanistic models for wind-dispersal, Soons *et al.* (2005) found that fruit terminal velocity measured in highly fragmented populations of *Cirsium dissectum* and *Salvia pratensis* suggested a very low probability of colonization of suitable patches of habitat. Quantification of the consequences of the variation in seed dispersal potential among landscapes for patterns of recolonization of *M. muralis* populations remains to be done.

Some measures of connectivity can reflect both the structure of suitable habitat, which is related to the cost of dispersal, and the patterns of occupancy of patches in favourable habitats, which could vary with dispersal limitation and extinction–recolonization dynamics. The association between V_t^{-1} and connectivity could thus reflect the fact that either a lower dispersal ability of seeds is selected for in the most isolated fragments or greater dispersal ability results in a less patchy distribution of individuals in the landscape. Note that in the first case, we expect genetic differences for seed dispersal ability among landscapes, while this is not necessary the case in the second scenario. The two scenarios are, moreover, not exclusive. The habitat requirements of *M. muralis* are specific enough in each region (see description of field sites and the Supporting Information), that we feel confident about the assumption

that unoccupied areas are generally unsuitable for its growth and establishment. This is particularly the case in the highly fragmented Spanish landscapes, since the favourable habitat in this region is well defined and indeed very limited to the infrequent moist habitats within vegetation gaps available in this dry southern Mediterranean area. The plant was systematically present in all these seemingly favourable habitats.

As reviewed in the Introduction, theoretical predictions for the evolution of dispersal differ depending on whether dispersal is compared across landscapes of different connectivity, or among patches within the same landscape. The present empirical study does not allow us to separate those two dimensions of fragmentation because each landscape was often represented by a single focal patch only; and variation in both connectivity and dispersal was not explored within a landscape. At the scale of the landscape, fragmentation (and thus larger distances among fragments) increases the mortality associated with dispersal, and theory predicts that dispersal is then selected against. However, fragmentation also results in higher genetic similarity among neighbouring plants and faster turnover of populations because of smaller population sizes, which, by contrast, are expected to select for increased dispersal. If we are to interpret the present findings in the light of these theoretical predictions, the decline in seed dispersal potential with fragmentation in *M. muralis* (V_t^{-1} , present study) and in *C. sancta* (proportion of achenes with a pappus; Cheptou *et al.*, 2008) suggests that the effect of increasing dispersal cost far outweighs the other consequences of fragmentation in those plant populations. At the patch scale, models predict that isolation should be associated with lower dispersal in old populations but with higher dispersal ability in recently founded populations. Accordingly, the decline in V_t^{-1} with increasing patch isolation in Spain would be consistent with these predictions if the patches sampled have persisted isolated in the landscape for a long time and the rate of population turnover is low.

Mean dispersal ability (V_t^{-1}) of seeds was found to increase from south to north. It was in particular higher in Sweden, which was the most recently colonized (Chauvet *et al.*, 2004). This is consistent with theoretical predictions of dispersal evolution along expansion (the leading edge hypothesis; Hewitt, 1996; Travis & Dytham, 2002; Dytham, 2009) and with empirical results in other plant species (Cwynar & MacDonald, 1987; Darling *et al.*, 2008). As the mean landscape occupancy also increases with latitude in our data set, it is hard to disentangle the respective role of population history and fragmentation in explaining variation in seed dispersal. Yet, variation in occupancy does not explain completely the variation between regions for dispersal traits. For the same level of fragmentation, Swedish landscapes harbour more dispersive phenotypes than southern European populations. This last finding is consistent with the notion that population history plays an important role in explaining variation in dispersal in addition to landscape fragmentation.

In conclusion, phenotypic patterns of variation in seed dispersal traits in *M. muralis* are consistent with predictions about the evolution of dispersal in fragmented landscapes (Darwin's wind hypothesis), and in expanding populations (the leading edge hypothesis). More precisely, seed dispersal potential (V_t^{-1}) was found to increase with connectivity and in the most recently colonized populations. The present study thus highlights that our understanding of the effects of fragmentation may be increased by the consideration of historical factors. However, a more thorough examination of the previous evolutionary scenarios would require systematically investigating genetic variation of dispersal traits in landscapes with variable connectivity and recolonization history.

Acknowledgements

This study has been carried out with financial support from the Commission of the European Community, Energy, Environment and Sustainable Development (EESD) specific RTD programme EVK2-CT-1999-00037 'Dynamics of plant dispersal-related traits in fragmented European habitats: consequences for species survival and landscape management'. Research was also funded in part by the Institut Universitaire de France, the French National Agency for Research (contract ANR-05-BDIV-014), the Netherlands' Ministry of Agriculture, Nature and Food Safety, the Spanish research program Consolider-Ingenio Montes (CSD2008-00040), and The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS 3/2001-4151). We thank Sandrine Maurice and Ran Nathan for stimulating discussions, and Roger Pascual, Juan Carlos Matamala and Carles Palau for their help in field work. This is publication ISEM 2009-062 of the Institut des Sciences de l'Evolution, Montpellier.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Notes S1 A detailed description of the *Mycelis muralis* sites.

Fig. S1 Flowering and fruiting flower-heads of *Mycelis muralis*.

Fig. S2 A map of the study regions.

Fig. S3 Mean V_t^{-1} (+ SE) values per landscape in each of the regions considered at the European scale.

Table S1 Description of the European landscapes selected

Table S2 Summary of empirical studies investigating variation for dispersal ability in plants

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