

## REVIEW AND SYNTHESIS

# How is dispersal integrated in life histories: a quantitative analysis using butterflies

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### Abstract

As dispersal plays a key role in gene flow among populations, its evolutionary dynamics under environmental changes is particularly important. The inter-dependency of dispersal with other life history traits may constrain dispersal evolution, and lead to the indirect selection of other traits as a by-product of this inter-dependency. Identifying the dispersal's relationships to other life-history traits will help to better understand the evolutionary dynamics of dispersal, and the consequences for species persistence and ecosystem functioning under global changes. Dispersal may be linked to other life-history traits as their respective evolutionary dynamics may be inter-dependent, or, because they are mechanistically related to each other. We identify traits that are predicted to co-vary with dispersal, and investigated the correlations that may constrain dispersal using published information on butterflies. Our quantitative analysis revealed that (1) dispersal directly correlated with demographic traits, mostly fecundity, whereas phylogenetic relationships among species had a negligible influence on this pattern, (2) gene flow and individual movements are correlated with ecological specialisation and body size, respectively and (3) routine movements only affected short-distance dispersal. Together, these results provide important insights into evolutionary dynamics under global environmental changes, and are directly applicable to biodiversity conservation.

### Keywords

behaviours, dispersal, evolutionary constraints, global change, habitat fragmentation, life-history evolution, metapopulation dynamics, migration, morphology, phylogeny.

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## INTRODUCTION

Dispersal, the meta-behaviour ultimately responsible for gene flow (Ronce 2007), combines a suite of behaviour interrelated through cost/benefits relationships at each step of the dispersal process: before or at emigration, during transfer and at or after settlement (Clobert *et al.* 2009; Bonte *et al.* 2011). Dispersal is a key process for species functioning and persistence under those environmental changes that requires a spatial response of populations, like for instance, to track a shifting climate niche or to maintain connections among populations in increasingly fragmented landscapes, and it is also central to biotic invasions (Hanski & Gilpin 1997; Dullinger *et al.* 2004; Berg *et al.* 2010; van Kleunen *et al.* 2010). Accordingly, increasing effort has been made to understand the forces and constraints that shape the evolution of dispersal (Ronce 2007; Clobert *et al.* 2008; Phillips *et al.* 2010), and the conditions and contexts that modulate its expression (Clobert *et al.* 2004, 2009). Identifying which life-history traits co-vary with dispersal-related traits is therefore a first step in understanding how dispersal evolves according to selection pressures generated by accelerated environmental changes. Knowledge of relationships between dispersal and other life-history traits may also enable us to make predictions in

cases where dispersal abilities are unknown. This is particularly relevant for species requiring urgent conservation action, such as threatened species where detailed dispersal data are typically lacking.

The aim of this study was to investigate how dispersal is integrated into the life-history of organisms. Hence, we tested for correlations between various dispersal-related traits and life-history traits. These correlations will drive or constrain the evolution of dispersal in changing environments. We compiled information from available literature to identify a suite of life-history traits that potentially correlate with dispersal, either because theory predicts that their respective evolutionary dynamics are inter-related, or because of an expected causal link. We found theoretical support for a possible link between dispersal and a variety of species-specific traits, including demographic traits, ecological specialisation, behaviours involved in routine movements (like foraging) and morphology (see next section).

We addressed this general issue using butterflies as a model system. Butterflies are well suited for quantitative studies of dispersal (Hughes *et al.* 2007; Stevens *et al.* 2010b), and are excellent model organisms for ecology and evolution, as their ecology, life-history and morphology are well researched (Watt & Boggs 2003; Ehrlich & Hanski 2004). Stevens *et al.* (2010a,b) previously constructed a database with

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published information on dispersal in European butterflies. Herein, we added published information on life-history traits to investigate the patterns of co-variation between selected traits and dispersal. Comparative studies on several species cannot ignore phylogenetic relationships among species. However, in the particular case of butterflies, we also expect ecology to play an important role in shaping dispersal (Pavoine, S., Baguette, M., Stevens, V.M., Leibold, M.A., Turlure, C. and Bonsall, M.B., unpublished). Therefore, we performed our analyses accounting for phylogenetic non-independence and then used species as independent points.

Herein, we tested a number of hypotheses about predicted relationships between life-history traits and various dispersal measures. First, we discuss the theoretical predictions that will allow us *a priori* to select relevant traits. Next, we present the quantitative analyses of the relationships among the traits.

**Table 1** Summary of the main theoretical expectations on inter-dependency of several facets of the dispersal process and other traits, contrasted to the pattern of co-variations indeed found in butterflies. +: positive correlation between a trait value and the dispersal ability, -: negative correlation. Each trait is informed for  $N = 19\text{--}138$  species. Eight different measurements were considered for mobility, of which four directly informed for dispersal ability; 20 other traits and the phylogeny were considered as dependent variables in the analyses of butterfly dispersal

Trait	Mechanism invoked for a correlation with dispersal	Correlation predicted from theory	Dispersal trait(s) predicted to co-vary	Observed relationship	Dispersal trait(s) that co-vary
r-strategy	Dispersal and r-traits are coadapted to face habitat instability	+	All	++	Most
Fecundity	Kin competition favours the evolution of dispersal	+	Frequency, propensity	+ ?	Most
Lifetime	Allocation trade-off or antagonistic pleiotropy	-	Distance	- ?	Most
Growth rate	Allocation trade-off or antagonistic pleiotropy	-	Distance	+ ?	Most
Generation time	Gene flow per time unit is correlated with the generation time	+	Gene flow	+ ?	Most
Flexibility	Diapause and dispersal are alternative strategies to escape unsuitable conditions	-	Frequency, propensity	Null	
Capital breeding	Capital breeders allocate no part of adult-acquired resources to egg maturation	+	Distance	Null	
Flight period	Dispersal of mated females in capital breeders	+	Gene flow		
	Weight handicap for capital breeders	-	Distance		
Generalism	Reduced dispersal costs due to increased dispersal time window	+	Distance	Null	
	Interacting evolutionary dynamics of dispersal and habitat specialisation	+(or non-linear)	Frequency, Distance	+	Gene flow
Myrmecophily	Increased dispersal cost related to coarser spatial grain for specialists	+	Distance		
	Dispersal compensates for resource scarcity in specialists	-	Frequency, propensity		
Body size	Dispersal costs related to the opportunity of en route nectaring	+	Distance		
	Coarser spatial grain for myrmecophilic species	-	Distance	Null	
Male mate searching behaviour	Metabolic flight costs per unit weight are constant	+	Distance	++	Frequency of long-distance dispersal
Laying precision				+	Dispersal propensity, mean dispersal distance
Laying strategy	Dispersal is a by-product of routine movements (searching for mates)	+(in interaction with specialisation)	Distance	Null	
	Conflict in time allocation	-	Distance	Null	
Phylogeny	Dispersal is a by-product of routine movements (searching for host plants)	-(in interaction with specialisation)	Frequency, distance	-	Mean dispersal distance (direct effect)
	Kin competition favours dispersal evolution	+	Frequency		
Phylogeny	Conflict in time allocation	+	Distance		
	Habitat filtering is more important in shaping traits than phylogenetic constraints	Low	All	High	Vagrancy
				Null	All other mobility measurements

## THEORETICAL PREDICTIONS

Life histories are suites of morphological, developmental or behavioural traits that shape an organism's course from birth to death (Ronce & Olivieri 2004). These traits are connected by trade-offs and co-adapted as they are shaped by natural selection, to maximise fitness under particular environmental conditions (Stearns 1992; Roff 2002). Several facets in the life history of an organism may be linked with dispersal (see a summary in Table 1).

## Demography

Some studies showed that dispersal, together with other life-history traits such as a high intrinsic rate of population increase or a short generation time, is correlated with disturbed habitats (Shapiro 1975).

This is in accord with the theoretical prediction that the spatial-temporal variability in habitat quality has the propensity to initiate the evolution of dispersal (Gadgil 1971; Roff 1975; Comins 1980; McPeck & Holt 1992). Hence, dispersal can be viewed as an adaptation of species that inhabit varying environments (Tauber *et al.* 1986), where natural selection is expected to produce a suite of life-history traits (*r*-type strategy) that co-evolve with dispersal to allow species persistence (Dingle 1996). Consequently, we expect dispersal behaviours to co-vary with others *r*-selected traits.

Furthermore, some authors argued that correlations between fitness-related traits should usually be negative due to antagonistic pleiotropy (Rose 1982) or due to the allocation of limiting resources between competing traits (Mole & Zera 1993), as in the trade-off between fecundity and flight ability of insects (oogenesis-flight syndrome: Johnson 1969). Accordingly, we may expect a negative relationship between dispersal and most fitness-related traits such as survival or development times. However, some studies challenge such predominantly negative correlations among traits, suggesting that positive, negative as well as the absence of any correlation may also occur (Houle 1991).

Dispersal was also predicted to correlate with fecundity, as dispersal may evolve due to kin competition (Hamilton & May 1977; Clobert *et al.* 2004; Bowler & Benton 2005; Ronce 2007), and kin competition will be higher for species with high fecundity. Similarly, larvae hatching from egg batches should face stronger kin competition than those hatching from eggs laid singly, with consequences for dispersal evolution. Therefore, egg-laying strategy should also be considered.

A species' ability to maintain gene flow across space should depend on the generation time: species with a short generation time have more opportunities per time unit to make genetic connections among populations. Hence, we expect dispersal efficiency (the transformation of individual movements into gene flow) to correlate with generation time.

Development time (ontogeny) may be an opportunity to invest in reproduction, or not. In capital breeding butterflies, females have a short maturation time and a large proportion of full-grown eggs at emergence. Income breeders adopt the opposite strategy as they rely on adult resources to develop eggs (O'Brien *et al.* 2004). In capital breeders, females have more energy (acquired as adults) to allocate to dispersal movements than species with an income breeder strategy, which allocate a proportion of this adult-acquired energy to egg maturation. Moreover, in capital breeders, mating usually occurs just after female emergence, and females thus have a high probability of mating before dispersal. This will increase the chances of gene flow as a dispersing female will probably lay a larger proportion of her eggs after dispersal, and will move both male and female gametes. We thus expect capital breeders to have higher dispersal efficiency and longer dispersal distances. However, in extreme capital breeders, emerging females might be impeded to fly due to the extra weight of their egg loads, which may disproportionately increase dispersal costs, modifying the relationship between dispersal and the egg maturation strategy.

Species with a long flight period should also show longer dispersal distances and at higher frequencies. A long flight period results from either all individuals being on wings for a long time (long adult lifetime) or from individuals emerging asynchronously. In several butterflies, when emergences are staggered, males emerge before females (protandry). Consequently, male–male competition can be high at the beginning of the flight period, which may in

turn increase dispersal frequency (Odendaal *et al.* 1989; Baguette *et al.* 1998). Moreover, asynchrony (and protandry) has been shown to enhance Allee effects in small populations through increased female matelessness (Calabrese *et al.* 2008). Dispersal may compensate for this effect by increasing mating opportunity across local populations with uncoupled dynamics, increasing the benefit of longer dispersal distances for highly asynchronous species. Alternatively, long flight periods might simply reduce dispersal costs during transfer by increasing the opportunity to experience suitable weather conditions that allow dispersing at lower physiological costs. Therefore, we predict a positive relationship between the flight period and both the dispersal propensity and the dispersal distance.

### Specialisation

Two different causal mechanisms may correlate dispersal to ecological specialisation. Dispersal could constrain the evolution of specialisation or, on the contrary, specialisation may act on the evolution of dispersal. In this latter case, we expect the disperser phenotype to spread among generalists and to be counter-selected for in specialists. This is so because, in specialists, the spatial grain of ecological resources is coarser than in generalists, and hence, dispersal costs should be higher at both the transfer and the settlement stages of dispersal (Baguette & Van Dyck 2007). However, we may also argue that high dispersal is a key trait for specialists allowing them to compensate for the scarcity of their resources (Samways & Lu 2007; Barbaro & van Halder 2009). To the best of our knowledge, there have been only a few attempts to investigate the evolutionary dynamics of dispersal relative to the degree of specialisation (Kisdi 2002; Nurmi & Parvinen 2011). Several studies (Brown 1992; Nurmi & Parvinen 2008) nevertheless tested the idea first proposed by Levins (1962) that very low dispersal rates and short dispersal distances generally encourage the evolution of local specialisation, whereas higher dispersal frequencies/distances result in the evolution towards generalism. However, non-monotonous relationships between dispersal and the evolutionary dynamics of specialisation are also possible, with both low and high dispersal favouring generalism and intermediate dispersal favouring specialists (Ronce & Kirkpatrick 2001; Kisdi 2002; Nurmi & Parvinen 2008).

### Body size

Dispersal ability may directly relate to body size. All other traits being equal, particularly the metabolic costs of displacement per unit of body weight, larger species may move further than smaller ones. There is evidence for such a relationship in mammals, birds and fishes (Paradis *et al.* 1998; Sutherland *et al.* 2000; Bradbury *et al.* 2008). So, we may predict a positive relationship between dispersal distance and body size.

### Behaviours

Dispersal may not be independent from other behaviours. Van Dyck & Baguette (2005) argued that two distinct movement types may lead to dispersal: specialised movements designed for net displacement, and routine movements in search for resources (food, mate, etc.). Hence, dispersal distance and dispersal frequency might correlate with

the extent and the frequency of routine-like movements. This relationship can, however, be conditional to the spatial grain of the resources as specialised displacements are predicted to make a more important contribution to dispersal than routine movements in specialised species, where resources have a coarse grained distribution (Baguette & Van Dyck 2007). Hence, we expect dispersal to be dependent on the interaction between specialisation, scaling the graininess of resources, and the extent and frequency of routine movements.

Several routine behaviours need to be considered in butterflies. First, male butterflies adopt a variety of mate searching strategies: they may either wait for encounters with females, or search for them by patrolling across the habitat. They can also form leks at meeting places with specific movement patterns. As actively searching butterflies have to move substantially more than species with a sit-and-wait strategy, this may cause increased dispersal distances. Also, variation in female behaviour can be significant as butterfly females vary in their oviposition behaviour. Females may lay eggs either singly or in batches. As mentioned earlier, this should impact the level of kin competition among larvae with putative effects on dispersal evolution. Furthermore, single-egg layers may require greater movement to select a series of individual host plants, and hence they may disperse more than batch layers as a by-product of these routine movements. Whatever the mechanism, the egg-laying strategy may thus correlate with dispersal frequency and dispersal distance. Independent of their laying strategy, females may be more or less precise in their oviposition site choice; some species select very precisely the part of the host plant on which each egg (or batch) is laid, whereas other species lay where they descend. The more time a female requires to select oviposition sites, the less time there is for other activities, including dispersal, which may cause laying precision to negatively correlate with dispersal distance.

## MATERIAL AND METHODS

### Dispersal database

Butterfly mobility has been assessed using a variety of methods (Stevens *et al.* 2010b). The most popular include mark-release-recapture (MRR) and population genetics using allozymes. For the sake of statistical power, we restricted our analyses to European species and to the eight mobility measurements in Stevens *et al.* (2010b) available for >15 species (Table 2).

We considered four mobility measurements as directly indicative of *dispersal* (movements susceptible to cause spatial gene flow). The four remaining were less directly related to dispersal as they could also pertain to routine movements or migration (seasonal change in the spatial distribution of a species). When we discuss all eight measurements together, we refer to the species' *mobility*.

The four measurements of dispersal were directly related to inter-patch movements assessed in MRR surveys or to spatial gene flow inferred using genetic methods, and they provide information about various aspects of the dispersal meta-behaviour: the *dispersal propensity*, the *mean dispersal distance*, the *frequency of long-distance dispersal* movements derived from MRR surveys and the *gene flow*, which provides information on dispersal efficiency.

The four other measurements also describe some aspects of butterfly mobility, but were not necessarily correlated with dispersal (Stevens *et al.* 2010b): the mean *daily displacement* corresponds to both intra- and inter-patch movements recorded in MRR; the *vagrancy* indicates if, and how frequently, a species was observed in an area without its host plants; the *migration* tendency ranks species according to the extent of their migration habits; and the *expert score* summarises expert knowledge on butterfly mobility. Although less reliable, this latter measurement was available for a large sample of species that were rather evenly distributed across the phylogeny.

**Table 2** Dispersal and mobility measurements for European butterflies, from Stevens *et al.* 2010a

	Mobility measurement	Description	Transformation	N*
Dispersal	Mean dispersal distance	Average distance of dispersal of individual butterflies (in km), estimated from the constant $\alpha$ of a negative exponential function of the form $P(D) = e^{-\alpha D}$ with $D$ = distance (km), fitted to dispersal kernel (density probability of dispersal distances) obtained from mark-release-recapture (MRR) surveys. The mean dispersal distance is $1/\alpha$ .	$x' = \log(1/x)$	30
	Frequency of long-distance dispersal	Probability of > 5 km dispersal movements, estimated from an inverse power function of the form $P(D) = a \cdot D^{-b}$ with $D$ = distance (km), fitted to dispersal kernel (density probability of dispersal distances) obtained from mark-release-recapture (MRR)	$x' = \log(x)$	28
	Dispersal propensity	Dispersal tendency estimated from the difference between all marked individuals and the proportion of recaptures occurring in the patch of initial capture (i.e. the fraction of residents) in MRR surveys. Corresponds to $[1 - \text{fraction of residents}]$ .	$x' = -\sqrt{x}$	25
	Gene flow	Effective dispersal estimated from gene flow across landscapes, as assessed by the observation of allozyme distributions. Corresponds to $1 - F_{ST}$ . $F_{ST}$ , the genetic structuring of populations inferred from genotypes at polymorphic allozymes, is inversely related to spatial gene flow. $1 - F_{ST}$ is thus proportional to gene flow among populations and informs dispersal efficiency.	$x' = 1 - \sqrt{x}$	26
Mobility	Daily displacements	Mean daily displacement (m) estimated from movements between successive captures in MRR. Takes also account from intra-patch movements.	$x' = \log(x)$	19
	Vagrancy	Indicates the relative frequency of butterfly sightings outside patches with suitable host plant(s) in transect surveys (Cook <i>et al.</i> 2001)	$x' = \log(x + 1)$	19
	Migration	Migration tendency, as estimated by Cook <i>et al.</i> (2001). The index is the sum of ranks for eight attributes, placed in order of magnitude: (1) ex-habitat vagrants, (2) suburban garden records, (3) urban, central business district records, (4) recorded range expansions, (5) at-sea records, (6) records of undertaking mass-movements, (7) evidence of overseas migration, (8) habitual seasonally reversed long-distance migrations.	$x' = \log(x)$	19
	Expert score	Mobility (both dispersal and migration) ranking by Bink (1992)	$x' = \ln(x)$	138

\*Number of European butterfly species for which the mobility measurement is given in Stevens *et al.* (2010b).



In mobility measurements derived from MRR and genetic surveys, several values per species were often available. In these cases, we retained the value that reflected the strongest mobility.

### Traits database

For information on butterfly traits, we mainly used Bink (1992) and Lafranchis (2000). Bink (1992) provides data on 19 traits for 142 species from N-W Europe. An additional trait, the egg-laying strategy, was extracted for 133 of those species from Lafranchis (2000), and for five additional species by searching the literature.

We used 11 life-history traits pertaining to species' demography: *potential* and *maximum fecundity*, *adult lifetime*, the *annual number of generations*, the *larval growth rate* (both for the first annual generation and averaged over successive generations), the *ripe egg load* at emergence, the *ovigeny index* (proportion of eggs matured at female emergence), the duration of *adult female maturation*, the *overwintering stage* and the *flexibility* of the life-cycle. All these traits were strongly inter-correlated (Appendix S1). Therefore, we summarised demography by the first three axes of a principal component analysis (PCA). This PCA was built on ten traits (detailed in Table 3). The flexibility of the life cycle was not included as it was binary, separating species with inflexible life-cycle from species with prolonged, shortened or repeated diapause, with facultative aestivation or with staggering of emergences, all considered 'flexible species'.

Four traits described species ecological specialisation: *thermal tolerance*, *adult habitat range*, *larval dietary breadth* and the strength of a mutual association with ants (*myrmecophily*). The first three traits were summarised by the first two axes of a PCA (Table 4) for further analyses. Myrmecophily was not included in this PCA, because it is strongly skewed to the family Lycaenidae (44 species of the 142 have associations with ants).

*Wing length* was the only morphological trait available in the dataset. Wing length was averaged by Bink (1992) over sexes and generations in cases where these were polymorphic.

Three behavioural traits were considered. For females, we retained the precision of oviposition behaviour (*female precision*) that ranged from 1: the female lays where it lands, or even when it is still flying, to 9: the female chooses the plant species, the tissue, the height and the orientation before laying. Secondly, we considered the female *laying strategy*, segregating single-egg layers from those species that lay batches of  $\geq 2$  eggs. For males, we retained seven levels in the strategy of *mate location*, from sit-and-wait strategy to lek forming, through neutral patrolling and territoriality.

Finally, our database reports on the length of the *flight period* for the first annual generation. Flight period results from the interplay between adult lifetime and the synchronisation of adult emergences, as shown by the low, but significant correlation between lifetime and flight period (Appendix S1).

**Table 3** Contribution of 10 butterfly demographic traits to the three-first axes of a PCA, and their correlations with these axes

Trait	Trait description	Relative contribution to PCA axes (%)			Correlation with PCA axes		
		Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Ovigeny index	Proportion of full-grown eggs at female emergence.	5.8	0.5	26.9	-0.47	-0.10	0.64
Female maturation	Duration (days) between female emergence and its first laying.	4.6	14.5	25.9	0.42	0.56	-0.63
Ripe egg load	Number of mature eggs in female's abdomen at emergence.	6.9	12.1	10.7	0.51	0.51	0.41
Potential fecundity	Mean number of eggs laid by females of the species.	17.3	6.2	6.5	0.81	0.36	0.32
Maximum fecundity	Maximum number of eggs a female of this species may lay.	17.2	4.3	7.8	0.80	0.30	0.35
Overwintering stage	Stage at which the species usually overwinters. Ranges from 0 (egg) to 6 (adult), and an additional category for species without overwintering (warm regions).	9.9	2.6	6.0	0.61	-0.24	0.30
Number of generations per year	Annual number of generations, from 0.5 (biannual species) to 3 generation/year	11.9	9.9	0.9	0.67	-0.46	0.12
Adult lifetime	Mean duration (days) of the adult stage. Upper limit set at 60 days for species overwintering as adults.	4.7	10.6	8.7	0.42	0.48	-0.37
Larval growth rate (1st annual generation)	Duration (days) of the feeding period for larvae (i.e. without diapause) of the first annual generation.	11.2	19.9	3.1	-0.65	0.65	0.22
Larval growth rate (averaged over generations)	Duration (days) of the feeding period for larvae (i.e. without diapause), averaged over the various annual generations.	10.5	19.3	3.5	-0.63	0.64	0.23

**Table 4** Contribution of three butterfly specialisation traits to the two-first axes of a PCA, and their correlations with these axes

Trait	Trait description	Contribution to PCA axes (%)		Correlation with PCA axes	
		Axis 1	Axis 2	Axis 1	Axis 2
Thermal tolerance	Degree of adult tolerance to temperature extremes and temperature variations.	43.8	6.7	0.78	-0.25
Adult habitat range	Number of different ecosystems in which adults are usually found.	44.4	5.2	0.79	-0.22
Larval dietary breadth	Number of different host plants caterpillars accept: Plants of one species, several species of the same genus, several genus of the same family or several families.	11.8	88.2	0.41	0.91

## Statistical analyses

The main goal of our statistical analyses was to detect whether dispersal measurements were correlated with other relevant traits in butterflies. We used analyses of variances, all performed with R (R Development Core Team 2011). We first built models where a given mobility measurement was considered as the dependent variable and other traits were proposed as explanatory variables. For MRR and genetic-derived measurements, the spatial scale of the study site was added as a covariate, as it may impact the measurement of dispersal (Schneider 2003; Stevens *et al.* 2010b). We used the longest distance between samples, except for daily displacements where the mean distance to nearest patch was retained. Next, we selected candidate models among all simpler models derived from the full model. We compared the candidate models by their Akaike Information Criterion, corrected for small sample sizes (AICc) (Burnham & Anderson 2002). We retained all models with  $\Delta\text{AICc} < 2.0$  from the model with lowest AICc. Dispersal measurements were unfortunately generally available for no more than 30 species (Table 2), which impeded us to include all main effects and their interactions in a single model (i.e. 12 variables + scale as a covariate). Therefore, we compared AICc of a first bulk of models with eight dependent variables. Then, we dropped all variables not retained by the AICc selection from this subset, and added the remaining variables and six interactions between specialisation (two PCA scores) and routine behaviours (mate location, laying strategy and female precision), and again selected the model(s) that best fitted the data. When several models had similarly low AICc ( $\Delta < 2$ ), they were averaged as implemented in the MuMIn R package and the statistical significance of each effect was appreciated by the observation of the confidence interval of its estimate.

The effects of phylogeny were accounted for using phylogenetic generalised least squares (PGLS). Pavoine *et al.* (unpublished) recently showed that a wide variety of life-history traits (including mobility) were both constrained by species phylogeny and by habitat filtering. In particular, their study of butterfly community assemblages supports the hypothesis that local environmental filtering may have driven character convergences in functional traits of species belonging to different clades. We therefore systematically compared models with phylogenetic relationships (PGLS) to models considering species as independent units (generalised linear models: GLM), using their respective AICc as an indication of their relative fit. We used the consensual phylogenetic tree provided in Cizek *et al.* (2006), and computed branch lengths using Grafen's (1989) method. Next, we pruned this tree that originally comprised 369 species so as to retain only the species for which the mobility measurement was available. Correlation structure was then calculated under the hypothesis of a Brownian motion, before being incorporated into the PGLS.

All the mobility measurements were transformed prior to analyses so as to conform or approach normality (Table 2). We, moreover, standardised all explanatory variables (except the two binary variables) to be able to compare the extent of their effects in GLM and PGLS.

## RESULTS

The three-first axes of the PCA applied to demography summarised cumulatively 74% of the variance in these traits, with, respectively, 38, 21 and 15% of the total variance (Table 3). The PCA applied to

specialisation traits summarised 79% of the variance in two axes representing 47 and 32% of the total variance respectively (Table 4).

## Correlates of dispersal and verification of theoretical expectations

Our results strongly supported the association of dispersal with demography (Table 5). This was particularly true for the first axis of the PCA on demographic traits, which positively correlated with six of the eight mobility measurements considered, although the relationship with daily displacements and gene flow was not significant (Table 5). This axis was, however, not retained in models for dispersal propensity or vagrancy.

Long-winged species had higher dispersal propensity, longer mean dispersal distances and higher frequency of long-distance dispersal than short-winged species. Experts also gave them higher scores.

Other significant relationships were less general across traits or mobility measurements (Table 5). Expert score was higher for generalist species, which also had significantly less genetic structuring among their populations (higher gene flow) and tended to migrate less than specialists. Compared with egg-batch layers, single-egg layers had significantly longer mean dispersal distances and higher expert scores. Butterflies with high scores on demographic axis 2 had higher long-distance dispersal frequencies. Unsurprisingly, the spatial scale over which they were measured also affected the mean dispersal distance and the daily displacements measured.

Contrary to what was predicted, several traits had no significant effect on mobility, regardless of the mobility measurement (see Tables 1 and 5). The specialisation x behaviours interactions also had no significant effect on mobility.

## Phylogenetic effect

Phylogeny had negligible influence on butterfly mobility: the PGLS-GLM comparison highlighted the low impact of phylogenetic relationships on the correlations among traits: GLM almost always outperformed PGLS in explaining the variance in butterfly mobility. The difference between the lowest AICc of a GLM and the lowest AICc of a PGLS was  $< -14$  for seven mobility measurements of eight. For vagrancy, however, the phylogenetic constraint was prominent, as only the phylogenetic correlation was retained in the best PGLS, which outperformed GLM ( $\Delta\text{AICc}$  with best GLM =  $-18.9$ ) and other PGLS models ( $\Delta\text{AICc}$  with second best PGLS =  $-4.1$ ).

## DISCUSSION

### Dispersal as a part of demographic strategies

Our analyses revealed a strong association between demography and the ability to disperse, or, more generally, to move. Although fecundity, maturation time and adult survival has not been reported in the same unit of time (hence some non-conventional associations among demographic traits arose), the first axis grossly describes the well known slow-fast continuum found in vertebrates (Gaillard *et al.* 1989; Clobert *et al.* 1998) where r-species are characterised by a high fecundity. Therefore, the high impact of demographic axis 1 on mobility measurements reinforces the idea that a high mobility is part of the r-strategy. Migration has been mentioned in this strategy, as a means to temporarily escape from unfavourable conditions

**Table 5** Summary of generalised linear models (GLM) and phylogenetic generalised least squares (PGLS) built to investigate the relationship between dispersal or mobility ability of butterflies (for a description of mobility measurements see text and Table 2) and their demographic traits, their degree of specialisation, their routine behaviours, the duration of their flight period and their morphology (for a description of traits, see text and Tables 3 and 4). Bold-typed estimates show significant effects (with zero outside the 95% confidence interval of their estimate)

Mobility measurement	Model type	Int.	Demography				Specialisation			Behaviours			Interact. with axis1 spec.		Covar. Spatial extent	Model performance				
			PCA axis1	PCA axis2	PCA axis3	Flex.	Flight period	PCA axis1	PCA axis2	Myr.	Wing length	Mate loc.	Lay. precis.	Lay. strat.		* lay. strat.	* mate loc.	R <sup>2</sup>	W	
Mean dispersal distance	GLM*	Est.	-0.73	<b>0.23</b>	-0.06	-	-	-0.15	-	-	-	<b>0.12</b>	-	-	<b>-0.31</b>	-	-	<b>0.14</b>	0.75	0.58
		LIC	-0.83	0.13	-0.15	-	-	-0.31	-	-	-	0.02	-	-	-0.55	-	-	0.04		
		u.IC	-0.63	0.33	0.02	-	-	0	-	-	-	0.22	-	-	-0.06	-	-	0.23		
Frequency of long-distance dispersal	GLM*	Est.	-2.21	<b>0.32</b>	<b>-0.30</b>	0.20	-	-0.28	-	-	-	<b>0.32</b>	-0.25	-	-	-	-	-	0.63	0.65
		LIC	-2.5	0.08	-0.54	-0.08	-	-0.71	-	-	-	0.06	-0.54	-	-	-	-	-		
		u.IC	-1.92	0.55	-0.07	0.48	-	0.14	-	-	-	0.58	0.05	-	-	-	-	-		
Dispersal propensity	GLM*	Est.	0.82	-	0.04	-	-	-	-	0.05	<b>0.08</b>	-	-	-	-	-	-	-	0.45	0.90
		LIC	0.76	-	-0.01	-	-	-	-	-0.1	0.02	-	-	-	-	-	-	-		
		u.IC	0.87	-	0.09	-	-	-	-	0.1	0.14	-	-	-	-	-	-	-		
Gene flow	GLM*	Est.	0.84	0.05	-	-	-	-	<b>0.05</b>	-	-	0.03	-	-	-	-	-	-	0.56	0.66
		LIC	0.8	0	-	-	-	-	0.01	-	-	-0.01	-	-	-	-	-	-		
		u.IC	0.88	0.09	-	-	-	-	0.1	-	-	0.06	-	-	-	-	-	-		
Daily displacement	GLM*	Est.	2.25	0.16	-	-	-	-	-	-0.10	0.09	-	-	-	-	-	-	<b>0.26</b>	0.84	0.65
		LIC	2.15	-0.01	-	-	-	-	-	-0.21	-0.22	-	-	-	-	-	-	0.15		
		u.IC	2.35	0.33	-	-	-	-	-	0.01	0.09	-	-	-	-	-	-	0.37		
Vagrancy	PGLS	Est.	-0.46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	NA	NA	0.82
		LIC	-1.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
		u.IC	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Migration	GLM	Est.	0.59	<b>0.05</b>	-	-	-	-	<b>0.03</b>	-	-	-	0.04	-	-	-	-0.05	NA	0.90	0.36
		LIC	0.56	0.04	-	-	-	-	0.01	-	-	-	< 0.00	-	-	-	-2.79	-		
		u.IC	0.62	0.06	-	-	-	-	0.05	-	-	-	0.08	-	-	-	0.01	-		
Expert score	GLM*	Est.	0.12	<b>0.24</b>	-	-	0.10	-	<b>0.17</b>	-	-	<b>0.05</b>	0.05	-	<b>-0.18</b>	0.04	-0.01	NA	0.60	0.53
		LIC	1.15	0.18	-	-	-0.2	-	0.11	-	-	0	< 0.00	-	-0.32	-0.1	-0.05	-		
		u.IC	1.32	0.3	-	-	0	-	0.22	-	-	0.11	0.1	-	-0.04	0.18	0.03	-		

\*GLM model resulting from the averaging of all models with  $\Delta AICc < 2.0$  from the model with the lowest AICc. Dash indicates a variable that was not retained in the model (interactions with no effect across all models not shown). NA indicates variables not proposed in the models. Int., intercept; Est, estimate; *LIC* and *u.IC*, lower and upper limits of the 95% confidence interval for the estimate; PCA, principal component analysis (see text for details); Myr, myrmecophily; Flex, Flexibility; Mate loc, Mate location; Lay. precis, laying precision; Lay. strat, laying strategy.

R<sup>2</sup>, is the pseudo-R<sup>2</sup>, calculated as the squared correlation between observed and predicted values.

W, model weight, or sum of weights of all concurrent models retained in the averaging (for GLM\*).

(Southwood 1988). Our results suggest that dispersal is another spatial mechanism involved in the r-strategy since dispersal kernels, indicative of the frequency of long-distance dispersal and of the mean distance of inter-patch movements, strongly correlated with the axis 1 of demography. This axis also marginally impacted gene flow (Table 5).

However, to what extent this relationship is causal remains to be elucidated. The comparative method used here is a powerful tool for detecting associations among traits across species (Pagel & Harvey 1988), but the interpretation requires caution as associations may be indirect or even non-adaptive, resulting, for instance, from epistasy or pleiotropic effects (Rose 1982). Dispersal, like migration, is supposed to evolve under conditions of habitat instability (Gadgil 1971; Roff 1975; Comins 1980; McPeck & Holt 1992; Travis & Dytham 1999). In butterflies, dispersal may thus have been selected by the same environmental pressures that shaped life-history strategies. In agreement with this hypothesis, Dennis *et al.* (2004) showed that butterfly mobility correlated with habitat disturbance (as measured by the host plants' generation time). They hypothesised that this pattern emerged from butterflies and their host plants having evolved under common environmental conditions. However, alternatively, migration could be the causal link between demography and dispersal. In this scenario, enhanced flight performances in migratory species might cause an

apparent link between dispersal and demography, even if only migration is selected for by habitat instability. There is support for this hypothesis in birds, where morphological traits (wing shape) relate to both migration and dispersal (Dawideit *et al.* 2009). Contrarily to that observed in birds, we found a direct effect of morphology (wing length) on dispersal, but not on migration. Nevertheless, in butterflies, there is some correlation between dispersal ability and migratory tendency (Stevens *et al.* 2010b). An indirect relationship might have arisen, but only if morphological or physiological traits other than wing length link dispersal to migration, and caused dispersal to evolve as a consequence of the evolution of migration. Hence, for the moment, we cannot discriminate between these two non-mutually exclusive hypotheses: dispersal evolved directly as a part of the r-strategy in response to habitat instability, or, alternatively, dispersal is facilitated in species with attributes allowing migration.

The positive relationship of mobility to r-selected traits invalidated the existence of a general mobility-fecundity trade-off in butterflies. Fecundity was positively correlated with demographic axis 1, which in turn positively correlated with mobility. Although the oogenesis-flight trade-off was evidenced in several insects (reviewed in Denno *et al.* 1989), there are also examples of high movement capacity associated with rapid development, early reproduction and high fecundity like we

showed here (Lavie & Ritte 1978; Hanski *et al.* 2006). The consequences of this result are discussed further (see below: Evolutionary consequences).

The effect of demographic axis 2 on the frequency of long-distance dispersal was only significant when the effect of demographic axis 1 was accounted for, which possibly indicates a disproportional contribution of those traits that contributed strongly to the second axis when compared with the first (i.e. larval growth rate, adult lifetime, and maturation time). These life-history traits are positively correlated with the second axis of demography, which in turn correlated negatively with the dispersal measurement. As such, our results indicate that long-distance dispersing species tend to be fast developing species. This was counterintuitive, as a long maturation could also have increased the frequency of long-dispersal movements. The opposite trend observed here corroborated the hypothesis that dispersal in butterflies probably evolved in part as a response to habitat instability within the 'fugitive species' syndrome (Tilman 1994).

Adult lifetime positively correlated with both axis1 and axis 2 of demography; as such we cannot directly assess the relationship of adult lifetime with dispersal (as those axes had opposite effects). This would require the collection of survival data within the right time scale to better establish its link with other demographic parameters as well as with dispersal. The hypothesis that lifetime should be traded-off against dispersal ability at the inter-specific level is thus still an open question. There is, however, empirical support for such a trade-off in the Glanville fritillary butterfly (Hanski *et al.* 2006).

The fact that demographic axis 3 did not correlate with mobility was surprising, but can be linked to the fact that this axis only accounted for 15% of the total variance in life-history traits. This can also be the net result of the antagonistic forces relating dispersal to capital breeding (Table 1): direct costs of movement may penalise capital breeders, as increased relative abdomen mass will reduce flight ability (Jervis *et al.* 2005). On the other hand, capital breeders could be advantaged as they have more opportunity to mate before dispersal, and to allocate adult-acquired resources to flight *versus* egg maturation (Dennis *et al.* 2003).

Contrary to what we expected, the length of flight period had no significant effect on dispersal. Hence, the hypothesis that dispersal costs might be reduced with an increased window for dispersal did not find support in butterflies.

### Dispersal and morphology

Dispersal allometry is variable in butterflies, depending on which mobility, measurement is considered. Wing length strongly related to the frequency of long-distance dispersal, more loosely with the mean dispersal distance and the dispersal propensity, and not at all with gene flow (Table 5). The assumed causal relationship between dispersal and wing length comes from studies where the potential effect of other traits was not controlled for. However, as already mentioned, body size correlates with many life-history traits through allometry (Blueweiss *et al.* 1978; Wiklund *et al.* 1987; Gaillard *et al.* 1989; Clobert *et al.* 1998; Garcia-Barros 2000). As we controlled for the effect of several of these traits, the effect of wing length may have been reduced.

Wing length is, however, strongly related to the frequency of long-distance dispersal of butterflies, even when controlling for the effects of other life-history traits. The body size effect on this dispersal measurement thus goes beyond life-history allometry. Rather, we

suspect that the metabolic cost of flight is the key behind this pattern: as the cost of flight per unit weight is very constant (Tucker 1970; Schmidt-Nielsen 1972), large species are probably able to move longer distances at relatively low metabolic costs. This clearly requires further research.

### Dispersal and specialisation

Species specialisation had noticeably weak relationships with dispersal, with (low) correlations only between the first axis of the specialisation-PCA and dispersal efficiency (gene flow). However, this result is important, as it indicates that the advantage to generalists resides in the successful transition from individual movement to effective gene flow. This relationship is thus probably attributable to the deferred costs, i.e. paid at or after immigration into the new habitat patch (Stamps *et al.* 2005; Bonte *et al.* 2011). Several mechanisms might increase the deferred dispersal costs for specialists. Attrition during transfer may be higher for species with narrow thermal tolerances, and attrition can reduce individual's attractiveness to potential mates or diminish life expectancy or fecundity (Bonte *et al.* 2011); species with narrow habitat selection may also suffer reduced fitness after immigration into sub-optimal habitats, while more habitat types are optimal for habitat generalists; and attrition costs may also be higher for species accepting few nectar sources, which may result in fewer feeding opportunities during transfer. Adult feeding generalism is, however, associated with larval dietary breadth in butterflies (positive and negative relationships were shown, depending on context and analytical procedures: Stefanescu & Traveset 2009), a trait with hardly any effect on specialisation axis 1 (but rather on the second axis, not retained in our best models) and independent from adult habitat range (Appendix S1). This discredits this last hypothesis that habitat generalists may benefit from more *en route* nectaring. Specialisation axis 1 is dominated by adult habitat range and adult thermal tolerance, with generalists having high scores. The advantage to generalists thus probably results from differences in performance after immigration related to thermal tolerance or habitat selection, a question that could be solved by the confrontation of field data on movement rates and individual performances, to genetic data informing the genetic components of dispersal.

It is noteworthy that specialisation, although uncoupled with dispersal movements and only loosely related to migration and gene flow, has a large impact on expert score. This may indicate that expert scoring is influenced by species specialisation. It is reasonable to think that an expert may overestimate the mobility of species seen in a large variety of habitats, and flying under wide ranges of temperatures, two traits positively correlated with the first axis of the specialisation-PCA.

### Dispersal and routine behaviours

Surprisingly, and contrary to our expectations, when routine movements affected dispersal, this was independent from ecological specialisation (interactions not shown in Table 5 were not significant). In line with our expectations, single-egg layers realised longer dispersal distances than egg-batch layers, probably because single-egg layers had to move more often to select their oviposition sites. Interestingly, the oviposition strategy only correlated with short-distance dispersal. Indeed, the mean dispersal distance was extracted from negative exponential kernels that best fit at relatively short distances (Baguette 2003). This might indicate that only small-scale inter-patch



movements can be realised as a by-product of routine movements. This difference in patterns related to short- and long-distance dispersal movement is in accordance with the findings of Hovestadt *et al.* (2011), showing the presence of mixed dispersal kernels in the butterfly *Maculinea nausithous*, which they hypothesised was the outcome of a mixture of two distinct processes: daily routine movement and genuine dispersal (Van Dyck & Baguette 2005). Such routine movements did not impact on the frequency of long-distance movements or gene flow, both of greatest importance for species spread, species persistence and metapopulation functioning (Baguette 2003; Schtickzelle *et al.* 2005a; Trakhtenbrot *et al.* 2005).

### Evolutionary consequences

Dispersal directly interacts with the adaptive response of species to environmental changes, as it is responsible for the spatial redistribution of genotypes (Ronce 2007). This meta-behaviour now faces increased selective pressures because of the conjunction of an increasing impact of those global changes that require a spatial response through increased dispersal, and the ubiquity of dispersal costs (Bonte *et al.* 2011). The fact that dispersal life-history trait relationships are highly variable among the dispersal measurements considered challenges the hypothesis that all behaviours related to dispersal have evolved jointly into a real dispersal syndrome (Clobert *et al.* 2009); rather, each element in the dispersal process has probably evolved partly independently from the others in response to uncoupled selection pressures (Baguette & Van Dyck 2007; Clobert *et al.* 2009), and will probably continue to do so in the future. We think that this pattern has resulted from the partly independent costs associated with the various dispersal steps (Baguette & Van Dyck 2007; Bonte *et al.* 2011).

Our analyses ignored within-species variation in dispersal behaviours and in other traits. However, these may be quite high (see Stevens *et al.* 2010a on the importance of intraspecific variation in dispersal). The strong correlations among traits may also constrain dispersal at the within-species level. For instance, Schtickzelle *et al.* (2006) showed contrasting dispersal behaviours in the butterfly *Boloria eunomia*, a pattern that paralleled the level of fragmentation in suitable habitats. It would be interesting to investigate how other traits behave along such a gradient of habitat fragmentation. If other trait values are selected for as a by-product of selective pressures imposed on dispersal behaviours, this may have strong effects on processes like local adaptation and speciation. Likewise, other environmental conditions may change the cost-benefit value of dispersal, like population density (Konvicka *et al.* in press), host plant distribution or climate. Investigating how the co-variations among traits vary according to these conditions at the population level certainly deserves further empirical investigation.

Dispersal consists of several behaviours, from the decision to leave, through the ability to move safely through inhospitable habitats, to navigate towards a suitable patch, to the settlement and the recruitment into this patch (Stenseth & Lidicker 1992; Ims & Yoccoz 1997). We showed that these components of dispersal may be partially decoupled in evolutionary and ecological times. Although related to movement rates, wing length has no direct effect on dispersal efficiency (i.e. gene flow) in butterflies. We observed the reverse for specialisation, which was related to gene flow, but not to individual movements. Accordingly, we suggest that individual movements and gene flow, two components of the dispersal process, might be

uncoupled under some circumstances. Furthermore, ordinary movements may result in small-scale dispersal, but have no significant effect on long-distance dispersal and gene flow. Hence, ecological or evolutionary changes in ordinary movements might impact local dispersal, but will probably have no effect on spatial gene flow, especially for long distances. Likewise, if the relationships between the frequency of long-distance dispersal and the second demographic axis (Table 5) is causal, or at least direct, an evolutionary change in development rate, like for instance, in response to climate change (Parmesan 2006), may result in a side-effect on the ability to move long distances.

Our comparative study helps identify which life-history traits covary with which dispersal traits; however, this study does not identify the causal mechanisms of these covariations. As such, further mechanistic studies testing the processes that explain the correlations are now warranted. Nevertheless, we may expect the evolution of longer dispersal distances to be slow for species with currently low dispersal ability, simply because these also tend to have low demographic turnover.

The fact that the relationships between dispersal and other life-history traits were highly variable among the dispersal measurements considered also suggests that the selective pressures acting on each of those components potentially may have decoupled effects on other traits. Noticeably, the dynamics of specialisation and effective dispersal will probably interact in populations facing changed spatial pressures, with consequences for community composition and functioning. Devictor *et al.* (2008) already showed that human-driven environmental changes result in biotic homogenisation. The link between the ability of a species to maintain gene flow and its specialisation will probably reinforce this homogenisation, as the consequence of an increased pressure for higher effective dispersal rates (as imposed by fragmentation and climate change). This would favour generalist species over specialists. Likewise, the presumed absence of an oogenesis-flight trade-off has important consequences for the evolutionary potential at invasion fronts, as both dispersal and demography may jointly evolve towards increased invasiveness.

Finally, our analyses showed evidence of low phylogenetic constraints acting on dispersal in butterflies, consistent with the observation of Pavoine *et al.* (unpublished) who quantified the relative importance of common ancestry and habitat filtering in shaping the evolution of butterfly traits (including the expert score we used) within a metacommunity, and who showed that habitat filtering has the dominant effect, whereas phylogenetic constraints were much lower. The strong association of dispersal and demography reinforces this idea that both demography and mobility are evolutionary labile traits, which have converged in distant clades subjected to common environmental constraints, for instance, habitat instability. There is, however, a possibility that the small sample sizes available for some mobility measurements did not reveal the phylogenetic constraint on the corresponding mobility trait.

### Consequences for species functioning under changed environmental conditions

The positive relationship between demography and dispersal ability has major implications for both species invasiveness and species persistence. Low rates of displacement through landscapes disfavour the persistence of species facing climate change or habitat fragmentation (Henle *et al.* 2004; Ockinger *et al.* 2010), although some authors

argue that butterfly species with intermediate dispersal levels would decline the most (Thomas 2000). Given that dispersal correlated with demography, the challenges imposed by habitat fragmentation or by climate change should disproportionately impact species with low demographic turnovers, as these species also proved to have low dispersal rates. Specialist butterflies should suffer more from these environmental changes than generalists, because they have developed low dispersal abilities. However, both a low turnover and a high specialisation *per se* predispose species to extinction (Henle *et al.* 2004; Barbaro & van Halder 2009). Together, the correlations among traits would thus globally increase the discrepancy between species at risk and species less at risk in face of global environmental changes.

The existence of a colonisation syndrome has been questioned in theoretical studies (Ronce *et al.* 2000). Our study provides evidence of such a syndrome in butterflies where the turnover of individuals within populations was positively correlated with dispersal ability. In the same vein, high growth rates predispose plants to invasiveness (van Kleunen *et al.* 2010). In butterflies, strong dispersal tends to be related to fast turnovers, which will reinforce the invasiveness of those species that have high values for both. The Large White butterfly (*Pieris brassicae*) has, for example, very high dispersal power and a very fast turnover. These traits probably worked together to produce its invasive success (Feltwell 1982).

### Consequences for the choice of substitute species

Accounting for species' dispersal ability is of primary importance to develop efficient conservation strategies under global environmental changes (Brook *et al.* 2000). The lack of dispersal has been recognised as a main limitation of models for predicting biodiversity patterns (Guisan & Thuiller 2005; Engler & Guisan 2009). If the relevant dispersal data are unavailable, modellers either assume that there is no dispersal, or, on the contrary they assume that dispersal is unlimited. The addition to these models of dispersal data, even if imprecise, will help reduce the uncertainty of their predictions (Engler & Guisan 2009). Therefore, an attractive solution should be using a substitute species, i.e. a species used on the assumption that it shows how the species of conservation concern might respond to a given environmental disturbance (Caro *et al.* 2005). The critical element in the choice of this substitute is therefore its similar response to the focal processes. Our results give some insights on how substitutes for dispersal ability should be chosen.

An intuitive idea has been choosing the most closely related species for which the information is available (as did Schtickzelle *et al.* 2005b). The low impact of phylogenetic relationships on butterfly dispersal questions whether that is a valid approach. Rather, we suggest that a species with comparable demography is in most cases the best choice. Then, if one wishes to gain insight into gene flow, the proximity in species specialisation and particularly in thermal tolerance and adult habitat range can be considered alternatively.

Wing length has also often been used as a proxy for species mobility (e.g. in Ockinger *et al.* 2010), which was justified by the widespread correlation between flight ability and body size (Paradis *et al.* 1998; Sutherland *et al.* 2000; Komonen *et al.* 2004). We may, however, wonder whether body size is a valuable proxy for dispersal traits. Dispersal might correlate directly with wing length. However, its value as a dispersal proxy might be artificially inflated by the allometry of other traits related to dispersal. We show here that the potential advantages of summarising dispersal by body size (wing length) is

reduced given that (1) wing length relationships are low for most dispersal measurements, (2) allometric traits may have either no relationship or an inverse relationship with dispersal and (3) several non-allometric traits correlated better with dispersal (noticeably the specialisation or the egg-laying strategy) (Table 5). Using wing length alone will probably be insufficient to accurately predict a species' dispersal ability. Hence, although inferring dispersal ability from wing length may be the 'least bad' solution for species for which information on other traits is unavailable, the precision of this prediction will be rather low for most components of dispersal. Likewise, Sutherland *et al.* (2000), using a positive relationship between mammal body size and dispersal distance, have tried to apply this correlation to predict the expected median or maximum dispersal distance for species of given body sizes. The predictive capacity of their correlation was rather low, indicating that body size is a poor predictor of mammal dispersal abilities. In butterflies, species of similar wing length, however, may be preferred as a substitute in cases where the frequency of long-distance movements is an issue.

### Generality of the patterns

It is difficult to generalise the patterns we observed in butterflies (i.e. a strong association of dispersal with demographic traits, variable effects of body size and low phylogenetic constraints) across different taxonomic groups. Several studies have examined the relationships between dispersal and other traits at the species level. However, both the dispersal measurements and the traits considered varied widely among these studies. To our knowledge, the relationship with demographic traits was only investigated in plants (Thomson *et al.* 2010), but only the dispersal mechanism was considered, whereas the frequency, the distance or the efficiency of dispersal were all ignored.

The allometry in dispersal distances was observed in several taxa: marine fishes, mammals and birds with larger adult size dispersing larger distances (Sutherland *et al.* 2000; Bradbury *et al.* 2008); and the dispersal distance is positively correlated with propagule size across a wide variety of actively dispersing organisms (Jenkins *et al.* 2007). These reviews ignored other traits (in particular, the demographic traits co-varying with dispersal in butterflies), and their results cannot be interpreted as evidence for a direct effect of body size on dispersal. Our study showed that this effect may exist for the frequency of long-distance dispersal, but not for gene flow. As not all other studies separately addressed these two components of dispersal, we cannot generalise at this stage about the pattern of dispersal allometry.

It seems that the phylogenetic dependency of dispersal has not been assessed *per se* before. Rather, in some comparative studies cited here, the correction for phylogenetic dependency was applied *a priori*, with a variety of methods (PGLS, family added as either a categorical or a random variable and phylogenetic independent contrasts), whereas in other studies phylogenetic dependence was not considered at all. Investigating how phylogeny constrains dispersal across taxa certainly deserves further attention as this comparison would help us better understand the patterns of dispersal evolution.

### CONCLUSION

Using the rich literature on butterfly dispersal, we highlighted a strong association between most components of this meta-behaviour and the demographic strategy of species. We also showed that body size has less impact on dispersal than previously thought, and particularly had

no impact on spatial gene flow, which is the ultimate motivation of dispersal. Routine movements only impacted short-distance movements and had no insignificant effect on gene flow, which, contrarily to movement rates, was constrained by adult specialisation. Another crucial result was the negligible constraint imposed by phylogenetic relationships. Taken together, these results are of direct applicability for biodiversity conservation, as they allow (1) adequate choice of a substitute species, (2) identification of species most at risk under habitat fragmentation and climate change and (3) identification of side-effects of the selective pressures imposed on various components of dispersal under those challenges. In addition, we have shown how the various components of dispersal might be under decoupled selective constraints, a subject that certainly deserves further attention, particularly to detect the cause of the relationships we observed between species traits.

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## AUTHORSHIP

MB and VMS designed the study, together with HVD. VMS collected the data. AT and VMS performed the analyses, with significant insights from JC and MB. VMS wrote the first draft of the manuscript after having discussed the results with MB. All authors substantially contributed to revisions.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Correlations between pairs of traits in European butterflies.

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