# A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy?

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## Summary

**1.** Dispersal ability of a species is a key ecological characteristic, affecting a range of processes from adaptation, community dynamics and genetic structure, to distribution and range size. It is determined by both intrinsic species traits and extrinsic landscape-related properties.

**2.** Using butterflies as a model system, the following questions were addressed: (i) given similar extrinsic factors, which intrinsic species trait(s) explain dispersal ability? (ii) can one of these traits be used as a proxy for dispersal ability? (iii) the effect of interactions between the traits, and phylogenetic relatedness, on dispersal ability.

**3.** Four data sets, using different measures of dispersal, were compiled from published literature. The first data set uses mean dispersal distances from capture–mark–recapture studies, and the other three use mobility indices. Data for six traits that can potentially affect dispersal ability were collected: wingspan, larval host plant specificity, adult habitat specificity, mate location strategy, voltinism and flight period duration. Each data set was subjected to both unifactorial, and multifactorial, phylogenetically controlled analyses.

**4.** Among the factors considered, wingspan was the most important determinant of dispersal ability, although the predictive powers of regression models were low. Voltinism and flight period duration also affect dispersal ability, especially in case of temperate species. Interactions between the factors did not affect dispersal ability, and phylogenetic relatedness was significant in one data set.

**5.** While using wingspan as the only proxy for dispersal ability maybe problematic, it is usually the only easily accessible species-specific trait for a large number of species. It can thus be a satisfactory proxy when carefully interpreted, especially for analyses involving many species from all across the world.

**Key-words:** body size, dispersal ability in butterflies, phylogenetic generalized least squares (PGLS), species-specific traits, wingspan as a proxy

## Introduction

Dispersal occupies a very important place in animal ecology, ranging from natal and breeding dispersal exhibited by mammals and birds, over resource searches by a variety of invertebrates, to mass migrations (Bowler & Benton 2005). Dispersal of individuals among subpopulations affects local adaptation, population and community dynamics and genetic structure (Doligez & Part 2008). Historically, dispersal would have affected the ability of species to colonize new habitats and expand their range (Lester *et al.* 2007). On a more recent time scale, dispersal can determine survival of a species in a patchy landscape. This ability assumes greater significance given the high degree of habitat fragmentation today (reviewed in Tscharntke *et al.* 2002).

Butterflies have been a favourite model system for the study of dispersal, because they are easy to work with, the natural history of most species is well known and they exhibit many variabilities in their dispersal capabilities (Stevens, Turlure & Baguette 2010). Most studies have been at the species level – to characterize dispersal as a process, the factors affecting it and its role in determining other species characteristics like range size (Lester *et al.* 2007), density and distribution (Cowley *et al.* 2001), and extinction proneness (Koh, Sodhi & Brook 2004). But, the scale at which dispersal has been studied has not been consistent. To avoid semantic issues, I have used the following definition: dispersal is any movement between habitat patches, with habitat patches defined as areas of suitable habitat separated in space from other such areas, irrespective of the distance between them (Bowler & Benton 2005).

Dispersal is usually 'condition dependent': organisms in a variable environment match their phenotype against the

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prevailing environment, and if the outcome of staying is reduced fitness, the individual is likely to disperse and seek better prospects (Ims & Hjermann 2001). Given the same set of extrinsic conditions like landscape and climate, some species, which possess suitable traits, will be better able to establish and successfully reproduce in a new habitat patch i.e. will have a higher 'dispersal ability'(Kokko & Lopez-Sepulcre 2006).

Among the intrinsic species-specific traits that have been established to affect dispersal ability, the most intuitive is body size. The correlation between morphological traits and dispersal ability has been established in experimental (Chai & Srygley 1990) and inferential studies (Kuussaari, Nieminen & Hanski 1996; Hill, Thomas & Blakeley 1999; Merckx & Van Dyck 2002), but it remains contentious. Among these morphological traits, wingspan is usually preferred as a surrogate for body size, especially when other data are not easily accessible (Cizek, Fric & Konvicka 2006). Some studies even use wingspan as a direct correlate of dispersal ability (Baguette, Petit & Queva 2000; Louy *et al.* 2007; Öckinger *et al.* 2010). This relationship needs to be formally validated.

The spatial configuration of suitable habitat patches is critical in determining dispersal ability, especially in case of species where adults prefer a single habitat type (Öckinger *et al.* 2010) and whose larvae exhibit feeding specialization (Brommer & Fred 1999). These two traits – larval host plant specificity and adult habitat specificity – can be considered together as 'niche breadth' and have been shown to affect dispersal ability (Koh, Sodhi & Brook 2004; Kotiaho *et al.* 2005). The number of generations per year (voltinism) and flight period duration can together determine the time available for dispersal. The two traits are related, but should be considered separately, because there are species with the same number of broods in a year, which fly for different periods of time. Finally, the strategy adopted by males of a species to locate mates can affect dispersal ability. Species where the males perch and defend sites territorially may disperse lesser than species where males fly continuously and patrol for flying females (Ehrlich 1984).

The factors affecting dispersal ability can interact with each other to influence it in a complex manner. For instance, wingspan is seen to correlate with larval host plant specificity in sphingid moths, with specialists being smaller (Lindström, Kaila *et al.* 1994; Brandle, Stadler *et al.* 2008). Larger insect species require more time for development and thus form fewer generations per year than smaller species (Cizek, Fric & Konvicka 2006). While there has been more discussion about the individual effect of the traits discussed earlier on the dispersal ability of a single species, or a small group of species, to my knowledge there has been no study that looks at all the traits together in a comparative analysis.

To summarize, this study will answer the following questions: (i) among the intrinsic traits that affect dispersal ability, which one(s) are the most significant? (ii) can one of these traits be used as a proxy for dispersal ability? (iii) do interactions between different traits affect dispersal ability? To answer these questions, I have analysed four data sets from literature using both unifactorial and multifactorial, phylogenetically controlled analyses to account for interactions between predictor variables and confounding effects of phylogenetic relatedness.

## Materials and methods

### DATA SETS

In all four data sets, the response variable was a measure of dispersal ability. The first (SET1) was compiled from 81 capture–mark–recapture (CMR) studies. In this data set, the mean distance dispersed (in metres; MDD) was used as a proxy for dispersal ability. For studies that presented MDD for males and females, the mean was used. When more than one study had reported MDD for the same species, only the study with the maximum study area was used, because MDD is directly proportional to study area (Schneider 2003; Stevens, Pavoine & Baguette 2010). The other three data sets were from publications that have scored butterfly mobility to give mobility indices (MIs). Bink (1992) assigned mobility ranks to butterflies of Western Europe, from one for very sedentary, to nine for highly mobile (SET2, $n = 139$; mobility scores information provided by Virginie M. Stevens). The remaining two data sets were compilations of questionnaires sent to butterfly experts. Cowley *et al.* (2001) have MIs for British butterflies, from one for sedentary to 40 for highly mobile (SET3, $n = 47$). Komonen *et al.* (2004) have MIs from one for sedentary to 10 for highly mobile for Finnish butterflies (SET4, $n = 76$). For these three data sets (SET2 to SET4), the mobility index was used as the response variable.

In all four data sets, species for which reliable information could not be gathered were excluded from the analyses. In case of SET1, studies that were manipulated or carried out in controlled conditions (Kuussaari, Nieminen & Hanski 1996; Conradt *et al.* 2000) were also excluded. Analyses were carried out with and without migratory species for all four data sets. As there were no significant differences in the results, the paper only deals with reduced data sets that do not contain migratory species (reduced data sets: SET1 $n = 58$, SET2 $n = 133$, SET3 $n = 43$ and SET4 $n = 67$). The final four data sets have been presented in Tables 1 to 4 in Appendix S1. The four data sets were analysed separately because the mobility measures were too different to be combined meaningfully.

### SCORING THE PREDICTOR VARIABLES

Experimental studies that have tried to establish the relationship between body size and dispersal ability have used several proxies for body size like wing loading capacity, thorax mass, wing length and wing area and also, several proxies for dispersal ability, like air speed, acceleration capacity and vagrancy (Chai & Srygley 1990; Dudley & Srygley 1994; Cook, Dennis & Hardy 2001; Berwaerts, Van Dyck & Aerts 2002; Turlure, Schtickzelle & Baguette 2009). For large-scale studies, wingspan has been preferred as a proxy for body size, because it is the most convenient to obtain (or measure) for many species at the same time (see Quinn *et al.* 1997; Dennis *et al.* 2000; Cowley *et al.* 2001; Koh, Sodhi & Brook 2004; Kotiaho *et al.* 2005; Kuefler *et al.* 2008; Öckinger *et al.* 2010). This study will do the same and use wingspan measurements (in millimetres) (data from Cizek, Fric & Konvicka 2006). The expectation is for species with larger wingspans to have higher dispersal ability.

Niche breadth was scored as two factors. Larval host plant specificity was scored in three levels, according to the degree of feeding

specialization of the larvae (scoring method from Komonen *et al.* 2004) (1) monophagous that feed on a single plant species, (2) oligophagous that feed on one genus and (3) polyphagous that feed on at least one family of food plants. Adult habitat specificity was scored into two classes: 1 – specific to a single biotope; 2 – found in many biotopes. Species with monophagous larvae, restricted by the distribution of host plants, and species specific to a particular habitat, restricted by availability of suitable habitat, will probably have lower dispersal ability.

Mate location strategy was scored as 1 – patrolling and 2 – perching, based on the behaviour of males. Perching males can be expected to have restricted dispersal ability. Voltinism had three levels: 1 – exclusively univoltine (one brood per year); 2 – more than one generation per year even if only in part of their range; and 3 – multivoltine, occurring throughout the year in warmer parts (data from Cizek, Fric & Konvicka 2006). Flight period duration was scored as follows: 1 – one month or lesser; 2 – 2 to 4 months; and 3 – more than 4 months. Species that fly for a longer time, owing to multiple generations and/or a longer flight duration, can be expected to disperse to a greater extent. A list of information sources for the predictor variables is given in Appendix S1.

### DATA ANALYSES

Unifactorial analyses for the effect of each predictor variable on dispersal ability involved linear regressions between wingspan and MDD (SET1) or mobility index (SET2, 3 and 4) and analysis of variance (ANOVA) for the other variables. The magnitude of the effects of each predictor was evaluated using effect size statistics, to facilitate comparisons between the predictors for each data set and between data sets. Pearson's correlation coefficient $r$ was calculated for the regressions and Cohen's $d$ for the ANOVAs (Nakagawa & Cuthill 2007), using the web-based Practical Meta-Analysis Effect Size Calculator (Lipsey & Wilson 2001). Variables were transformed where necessary. Multifactorial analyses were carried out to get a minimum adequate model (MAM) through model simplification by backward deletion, starting from a maximal model that included all the six factors, and two-way interactions. Multiple regressions using analysis of covariance (ANCOVA) were used for all data sets except SET2, for which a generalized linear model (glm) with Poisson errors and a logit link function was performed.

The phylogenetic generalized least squares (PGLS) method was used to control for the effects of phylogenetic relatedness (Hansen & Martins 1996; Martins & Hansen 1997). This method incorporates information about relatedness (provided as a phylogenetic tree) into the error term of a generalized least squares (GLS) model, assuming a model of trait evolution. This model can be Brownian (trait evolves at a constant rate) or an Ornstein–Hulhenback (OU) process (trait is under selection). All data sets were tested for both models, and the OU model was the best fit for all. For input into the analyses, phylogenies were manually constructed, based on the latest available information from the Tree Of Life website (Tree of Life Web Project 2010). As the phylogeny was not fully resolved in some cases, the branch lengths were always set to 1 during the analysis. In all cases, a reduced data set was used for the PGLS analysis because phylogenetic information was not available for all species (SET1 $n = 54$, SET2 $n = 128$, SET3 $n = 47$ and SET4 $n = 67$).

The effects of phylogenetic relatedness on the data set was assessed using two parameters: a likelihood ratio test (LRT) comparing the PGLS model with a linear model with the same fixed effects structure but no phylogenetic information (Isvaran & Clutton-Brock 2007) and the parameter $\alpha$ (Hansen & Martins 1996). $\alpha$ is a measure of the rate at which the correlation between species decreases with phylogenetic distance. A low value of $\alpha$ means that the correlation falls slowly, indicating that the trait is conserved. If the PGLS was significant, the effect of individual factors was assessed using conditional *F*-tests (Isvaran & Clutton-Brock 2007). Fixed effects of model parameters were also estimated using LRTs to assess the differences between models after sequentially deleting significant terms from the minimal PGLS model and adding non-significant terms.

All analyses were carried out in the statistical language R, v. 2·12·1 (R Development Core Team 2010). The PGLS analysis was performed using the package APE (Paradis, Claude & Strimmer 2004) for the trees and the function gls in the package nlme (Pinheiro *et al.* 2010).

## Results

In SET1, the MDD ranged from 23 m in *Lycaena arota,* to 600 m in *Erebia epipsodea*. A significant number of species in the data set fall in the category of moderate dispersers, with MDD between 100 and 400 m (average of 200 m). This was true for the other data sets as well, with many species clustered around an average mobility index (four for SET2 where the range is 1–9, 20 for SET3 where the range is 1–40 and 5 for SET3 where the range is 1–10). The data sets cover species across all families, especially the region-wise data sets SET2, SET3 and SET4. Nevertheless, phylogenetic relatedness has a significant effect on the analysis only in SET3 ($\alpha = 0.37$, $P = 0.02$).

The results for the unifactorial analyses have been presented in Table 1. Effect sizes have been categorized as 'small', 'medium' and 'large' ($r = 0.1, 0.3, 0.5$ and $d = 0.2$, $0.5, 0.8$, respectively), based on Nakagawa & Cuthill (2007). Regressions between wingspan and dispersal ability are not only significant, but also have large, positive effect sizes and low Class Intervals (CIs) in all data sets, especially in SET2 and SET4 (Fig. 1). But, the predictive power of wingspan is inconsistent across data sets, from 7% (SET2) to 47% (SET3). Host plant specificity categorizes dispersal ability into groups that are significantly different from three data sets, with monophagous species having low dispersal ability (Fig. 2a). But, the effect size is small in SET2, bordering on medium in SET1 and medium with a very large CI for SET4. ANOVA for voltinism is significant in three data sets, well supported by large effect sizes in two, and a medium effect size in one, showing that species with more generations in a year can disperse to a greater extent (Fig. 3b). Species that are on the wing for longer periods disperse to a greater extent, because flight period duration has a positive effect on dispersal ability in the same three data sets (Fig. 3c). Adult habitat specificity is significant in two data sets (Fig. 2b), and mate location strategy only in SET1 (Fig. 3a), all with medium effect sizes.

Owing to the high number of contrasts, PGLS models are shown rather than linear models in the multifactorial analyses (summarized in Table 2). The results for linear and PGLS models are the same for all data sets except SET3, but the model parameters are different. Linear models are given in Appendix S3, Table 1. The minimal model for predicting dispersal ability had two factors in all data sets. Wingspan was

**Table 1.** Results of unifactorial analyses between each predictor variable and butterfly dispersal ability

| Data sets | SET1 | SET2 | SET3 | SET4 |
|---|---|---|---|---|
| **Linear regression between wingspan and MDD (SET1) or MI (SET2, 3 and 4)** | | | | |
| $P$ | **0·007** | **0·034** | **< 0·001** | **< 0·001** |
| $r^2$ | 0·11 | 0·07 | 0·47 | 0·13 |
| ES ('r') | 0·62 (L) | 0·87 (L) | 0·68 (L) | 0·84 (L) |
| (CI) | (0·48–0·73) | (0·82–0·91) | (0·47–0·81) | (0·75–0·9) |
| ANOVAS **for the effect of other predictor variables on MDD (SET1) or MI (SET2, 3 and 4)** | | | | |
| 1. Larval host plant specificity | | | | |
| $F$-value | $F_{(2,52)} = 6·86$ | $F_{(2,130)} = 3·54$ | $F_{(2,40)} = 1·12$ | $F_{(2,61)} = 3·78$ |
| $P$ | **0·002** | **0·031** | 0·337 | **0·028** |
| ES ('d') | 0·49 (S/M) | 0·35 (S) | 0·81 | 0·66 (M) |
| (CI) | (0·06–1·06) | (0·008–0·69) | (−0·14–1·76) | (0·17–1·15) |
| 2. Adult habitat specificity | | | | |
| $F$-value | $F_{(1,53)} = 5·09$ | $F_{(1,131)} = 3·99$ | $F_{(1,41)} = 0·64$ | $F_{(1,65)} = 1·96$ |
| $P$ | **0·028** | **0·047** | 0·428 | 0·165 |
| ES ('d') | 0·59 (M) | 0·42 (S) | 0·59 | 0·39 |
| (CI) | (0·06–1·12) | (0·06–0·77) | (−0·05–1·25) | (−0·09–0·89) |
| 3. Mate location strategy | | | | |
| $F$-value | $F_{(1,53)} = 4·70$ | $F_{(1,131)} = 0·54$ | $F_{(1,41)} = 0·67$ | $F_{(1,65)} = 0·50$ |
| $P$ | **0·034** | 0·462 | 0·416 | 0·481 |
| ES ('d') | 0·63 (M) | 0·13 | 0·25 | 0·37 |
| (CI) | (0·09–1·17) | (−0·21–0·47) | (−0·35–0·85) | (−0·10–0·86) |
| 4. Voltinism | | | | |
| $F$-value | $F_{(2,55)} = 1·83$ | $F_{(2,130)} = 13·89$ | $F_{(2,40)} = 3·89$ | $F_{(2,61)} = 4·49$ |
| $P$ | 0·169 | **< 0·001** | **0·027** | **0·015** |
| ES ('d') | 0·47 | 0·67 (M) | 0·82 (L) | 0·87 (L) |
| (CI) | (−0·21–1·15) | (0·29–1·04) | (0·18–1·46) | (0·28–1·46) |
| 5. Flight period duration | | | | |
| $F$-value | $F_{(2,52)} = 0·14$ | $F_{(2,130)} = 6·83$ | $F_{(1,41)} = 6·27$ | $F_{(2,61)} = 5·04$ |
| $P$ | 0·86 | **0·001** | **0·016** | **0·009** |
| ES ('d') | 0·15 | 0·51 (M) | 0·77 (L) | 0·50 (M) |
| (CI) | (−0·64–0·94) | (0·16–0·85) | (0·15–1·39) | (−0·0079–1·015) |

The significance (P-value) of each test is given, along with $r^2$ values for the linear regressions and F-values for the ANOVAS. Also, effect sizes are presented for each test, with Class Intervals (CI) in brackets. The effect size is given by Pearson's correlation coefficient 'r' for the regressions and Cohen's 'd' for the ANOVAS. The significant P-values ( < 0·05) are in bold. The effect sizes have been categorized as S – 'small', M – 'medium' and L – 'large' for $r = $ 0·1, 0·3 and 0·5 and $d = $ 0·2, 0·5 and 0·8, respectively, for the significant tests.

consistently retrieved in all four, flight period duration in two, and voltinism and host plant specificity in each one. No interaction terms were retained after model simplification. The predicted dispersal ability from the minimal PGLS models correlated significantly, but not tightly, with the observed dispersal ability (Pearson's correlation coefficient: SET1 $r = $ 0·46, $P < $ 0·0001; SET2 $r = $ 0·27, $P = $ 0·001; SET3 $r = $ 0·84, $P < $ 0·001; SET4 $r = $ 0·51, $P < $ 0·001).

## Discussion

### DATA SET COMPILATION

The four data sets used in the study have different measures of butterfly dispersal ability, with mean dispersal distance (MDD) in case of SET1 and mobility index (MI) in other data sets. There are unique problems associated with each measure. Most MDD values are based on only one short-term study carried out in one location per species, which usually underestimates the dispersal ability (Thomas, Wilson et al. 2002). This also means that the results from CMR studies and genetic measures like $F_{st}$ may not tally because genetic measures are indicative of historical gene flow, while patterns observed today can be very different, because of extensive habitat modification (Stevens, Turlure & Baguette 2010). The study areas used in MDD studies may not be large enough to effectively study dispersal ability of the species (Schneider 2003). The recapture probabilities also vary, from < 5% in some studies (Kuras, Benes et al. 2003; Auckland, Debinski et al. 2004) to above 60% in others (Sutcliffe, Thomas et al. 1997; Casula 2006). MDD studies can also confound routine foraging movements with special dispersal movements that are a result of a behavioural decision to disperse (Stevens, Turlure & Baguette 2010).

Stevens, Turlure & Baguette (2010) also examine other direct measures of dispersal, like the shape of dispersal kernels (exponential and power functions), patch connectivity (λ) and dispersal mortality. However, none of these measures are available for a large number of species, across many countries. In case of MDD studies in fragmented areas (some

**Table 2.** Minimum adequate models for each data set

| | Coefficient (SE) | t | P | LRT (on removal) |
|---|---|---|---|---|
| **a) SET1: minimum model** | | | | |
| log (Wingspan) | 1·168 (0·455) | 2·565 | 0·013 | P = 0·07 |
| Host | 0·315 (0·148) | 2·129 | 0·038 | P = 0·02 |

| | Coefficient (SE) | t | P | LRT (on addition) |
|---|---|---|---|---|
| *Non-significant terms* | | | | |
| (Intercept) | −0·078 (1·740) | −0·044 | 0·964 | |
| Habitat | 0·007 (0·240) | 0·032 | 0·974 | P = 0·488 |
| Mate | 0·151 (0·243) | 0·622 | 0·536 | P = 0·659 |
| Volt | −0·089 (0·162) | −0·550 | 0·584 | P = 0·293 |
| Duration | 0·392 (0·258) | 1·521 | 0·134 | P = 1·04 |

| | Coefficient (SE) | t | P | LRT (on addition) |
|---|---|---|---|---|
| **b) SET2: minimum model** | | | | |
| Wingspan | 0·067 (0·017) | 3·926 | 0·0001 | P = 0·0001 |
| Voltinism | 0·970 (0·194) | 4·992 | 0·1 | P < 0·0001 |

| | Coefficient (SE) | t | P | LRT (on addition) |
|---|---|---|---|---|
| *Non-significant terms* | | | | |
| (Intercept) | −0·543 (0·758) | −0·716 | 0·475 | P = 0·38 |
| Host | 0·210 (0·149) | 1·409 | 0·161 | P = 0·693 |
| Habitat | 0·241 (0·222) | 1·082 | 0·281 | P = 0·767 |
| Mate | 0·124 (0·209) | 0·593 | 0·553 | P = 0·645 |

| | Coefficient (SE) | t | P | LRT (on removal) |
|---|---|---|---|---|
| **c) SET3: minimum model** | | | | |
| (Intercept) | −49·896 (7·914) | −6·304 | 0 | |
| Wingspan | 1·524 (0·194) | 7·834 | 0 | P < ·0001 |
| Duration | 8·544 (2·406) | 3·55 | 0·001 | P < ·0001 |

| | Coefficient (SE) | t | P | LRT (on addition) |
|---|---|---|---|---|
| *Non-significant terms* | | | | |
| Host | 2·620 (1·633) | 1·604 | 0·116 | P = 0·036 |
| Habitat | 1·633 (2·146) | 0·761 | 0·451 | P = 0·102 |
| Mate | 4·133 (2·063) | 2·003 | 0·052 | P = 0·227 |
| Voltinism | 2·335 (1·562) | 1·494 | 0·142 | P = 0·160 |

| | Coefficient (SE) | t | P | LRT (on removal) |
|---|---|---|---|---|
| **d) SET4: minimum model** | | | | |
| log(Wingspan) | 2·362 (0·742) | 3·182 | 0·0023 | P = 0·0009 |
| Duration | 0·512 (0·330) | 1·551 | 0·026 | P = 0·006 |

| | Coefficient (SE) | t | P | LRT (on addition) |
|---|---|---|---|---|
| *Non-significant terms* | | | | |
| (Intercept) | −4·040 (2·681) | −1·507 | 0·137 | |
| Host | 0·159 (0·400) | 0·398 | 0·691 | P = 0·261 |
| Habitat | 0·400 (0·496) | 0·807 | 0·422 | P = 0·1983 |
| Mate | −0·239 (0·446) | −0·536 | 0·593 | P = 0·693 |

The effect of wingspan (WS), larval host specificity (Host), adult habitat specificity (Habitat), mate location strategy (Mate), voltinism (Volt) and flight period duration (Duration) on dispersal ability of butterflies (MDD in SET1 and MI in other data sets). Interactions between predictor variables were tested up to the two-way level, but none were significant ($P > 0·1$ in all cases). Fixed effects of the predictors were further assessed using likelihood ratio tests (LRT) after removing the term from the model for the significant terms and by adding them to the minimum model for the non-significant terms.

studies in SET1), routine movements are usually within a patch and dispersal events get recorded as interpatch movements, which aids in teasing apart these movements. Allozyme-based dispersal estimates were related to MDD from large areas; also, dispersal kernels that followed the inverse power function were related to MDD (Stevens, Turlure & Baguette 2010). The data set was compiled with care, choosing studies with the highest study area for each species and trying to obtain species information from the same paper or from the same region.

Mobility index (MI) values are averaged from many experts, and assume a different scale in each data set. Stevens, Turlure & Baguette (2010) have shown that the MI is a reflection of the migratory ability of a species rather than dispersal ability, because expert opinion is biased by confounding traits like wingspan, flight period duration, voltinism and phylogenetic relationships among species. But, they recommend using it as 'an indication of the relative dispersal ability' when a large data set is used, like in this case. Besides, migratory species have been removed, phylogenetic relatedness is controlled for, and the confounding factors mentioned above have been addressed by explicitly incorporating them into the analysis. Also, as described earlier, there are three data sets of MIs by region in literature, making it a valuable large-scale data base for butterfly mobility. Another advantage of MIs is that expert opinions are based on a variety of populations and timescales and are thus generalizable (Burke, Fitzsimmons & Kerr 2011).

The caveats attached to these data sets are reflective of the difficulty in measuring dispersal, especially in vagile taxa like butterflies. The advantage here is the availability of a single measure (MDD or MI) across many species, encompassing a wide geographic spread. This allows for a meta-analytic approach at no extra cost. I now examine the factors affecting dispersal ability keeping these caveats in mind, in the light of available literature, to synthesize what is known till now.

### WINGSPAN

The analyses clearly show that among the factors studied, wingspan is the most important trait affecting dispersal

ability. While the relationship is significant with large effect sizes for all data sets, one should exercise caution while extrapolating from wingspan to dispersal ability, because the predictive power of the regressions is low. The relationship has always been contentious in literature, with evidence pointing both ways. Experimental studies have demonstrated that wing length and thorax size affect flight ability and dispersal of Lepidoptera (Chai & Srygley 1990). Flight speed was also positively correlated with wing length, both in controlled and field conditions (Dudley & Srygley 1994; Berwaerts, Van Dyck & Aerts 2002). Turlure, Schtickzelle & Baguette (2009) showed that higher wing loading is associated with longer displacements in multiple species. Also, in a large-scale meta-analyses with insects, active dispersers with a larger wingspan were shown to attain greater maximum observed dispersal distances (Jenkins *et al.* 2007). There is a weak correlation between wingspan and mobility in Canadian butterflies (Burke, Fitzsimmons & Kerr 2011), though not in Swedish noctuid moths (Betzholtz & Franzen 2011).

Results from another set of studies allow one to explore the cause and effect of relationship between wingspan and dispersal ability *a posteriori*, by comparing populations with different histories. When newly established and permanent populations of *Pararge aegeria*, *Pyronia tithonus* and *Melitaea cinxia* (Kuussaari, Nieminen & Hanski 1996; Hill, Thomas & Blakeley 1999; Merckx & Van Dyck 2002) were compared, individuals were larger in newly colonized populations; but no such difference was observed in *Hesperia comma* (Hill, Thomas & Lewis 1996).

On the other hand, it has been shown that dispersal ability is correlated with physiology rather than morphological traits Hanski *et al.* (2002). Also, using only one trait as a surrogate for body size can be misleading; different suites of morphological traits can suit different flight patterns. Increased investment in thorax muscles and narrow, pointed wings can imply speedy but energetically demanding flight; large, rounded wings can imply long-endurance gliding flight (Fric, Klimova & Konvicka 2006).

This discussion goes to show that no definite relationship between wingspan and dispersal ability has been established
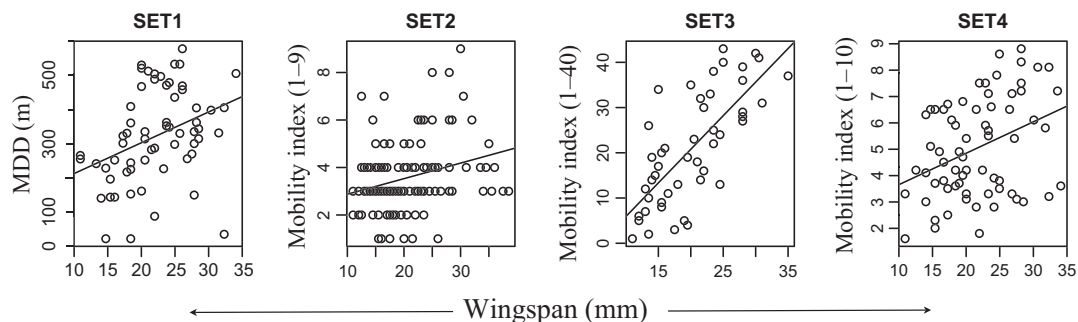


**Fig. 1.** Linear regressions between wingspan and dispersal ability for all data sets. In all the four graphs, wingspan (ws; given in mm) is on the *x*-axis and dispersal ability on the *y*-axis. Dispersal ability is mean distance dispersed (MDD; given in metres) in SET1 and mobility index (MI) in the other data sets. Note that SET2, 3 and 4 use different mobility indices. Log values on axes have been back transformed where necessary, for ease of comparison. The results for the regression analysis, along with details of transformations used, are as follows: SET1 [log(MDD) ∼ log(ws)]: $P = 0.007$, $r^2 = 0.11$; SET2 (MI ∼ ws): $P = 0.034$, $r^2 = 0.07$; SET3 (MI ∼ ws): $P < 0.001$, $r^2 = 0.47$; and SET4 [MI ∼ log(ws)]: $P < 0.001$, $r^2 = 0.13$.

thus far in literature. In spite of the doubt around this relationship, many studies have used wingspan as a proxy for dispersal ability (Baguette, Petit & Queva 2000; Louy *et al.* 2007; Öckinger *et al.* 2010). The regression analysis in the current study shows that the ability of wingspan to predict dispersal ability is low and varies according to the data set. But, the effect size calculations, which use the correlation coefficient, clearly establish the existence of a strong correlation between wingspan and dispersal ability in all four data sets. To conclude, I feel wingspan can be used as a proxy for dispersal ability, but cautiously. It can be exceptionally convenient in studies dealing with large numbers of species about which information is not readily available.

### NICHE BREADTH

#### Larval host plant specificity

Species where larvae feed on specialized food plants have lower dispersal ability, in three of four data sets in the unifactorial analyses (see Fig. 2a). Host plant specificity is also an important predictor of dispersal ability in the multifactorial analysis of SET1. It has been shown to predict mobility in Canadian butterflies (Burke, Fitzsimmons & Kerr 2011) and Swedish noctuid moths (Betzholtz & Franzen 2011). Also, larval diet breadth along with wingspan correlates with dispersal class in the sphingid moths of Indo-Australian tropics (Beck & Kitching 2007) and with migration rate in moths (Nieminen 1996).

Preference of a specific host plant restricts reproduction to patches that contain the host, in species like *Parnassius apollo* (Brommer & Fred 1999) and *Euphydryas editha* (Gilbert & Singer 1973). Samways & Lu (2007), in a study involving two sympatric species of the same genus, showed that the species with higher host plant specificity was threatened, while the other was not. Indirect evidence of the relationship between host plant specificity and dispersal ability can be seen among British butterflies, where species with monophagous larvae

are relatively rare (Hodgson 1993), and host plant generalists have a greater capacity for between island dispersal (Dennis *et al.* 2000). Among the Californian Lepidoptera, generalist species have been shown to have a greater tendency to use novel exotics as host plants (Jahner *et al.* 2011). Also, British butterflies with a narrower larval diet breadth have also advanced their date of first appearance to a greater extent (Diamond *et al.* 2011).

#### Habitat specificity

Preference for a particular habitat limits dispersal ability only in the unifactorial analyses in two of the four data sets and is not retrieved as an important predictor in any of the minimal models. This is quite surprising, given the large number of studies that have shown habitat to have a significant effect on movement patterns in butterflies. Field experiments have shown that spatial configuration of suitable habitat patches affects movement in butterflies (demonstrated in *Parnassius apollo* by Brommer & Fred 1999). Physical aspects of habitat boundary, such as increased foliar density or height, have been found to impede transitions between habitats for arthropods (Ries & Debinski 2001; Kuefler *et al.* 2008). Inhibitory behaviours at habitat boundaries (e.g. 'edge avoidance') may also constrain emigration in edge-sensitive animals (Schultz 1998; Haddad 1999; Merckx *et al.* 2003; Schtickzelle & Baguette 2003). A drop in dispersal ability in fragmented habitats has been documented in *Proclossiana eunomia* (Mennechez, Schtickzelle & Baguette 2003), a fact also corroborated by genetic studies (Lewis, Thomas *et al.* 1997; Vandewoestijne and Baguette 2004).

Habitat specificity does affect dispersal ability in the unifactorial analysis of SET1. This was expected, because many CMR studies in SET1 were performed to evaluate the response of species to fragmented habitat (see Appendix S1 and Table 1 for details). It is also significant in SET2, but not in SET3 and SET4. As the latter two have average MIs from expert opinions, the lack of pattern may reflect biased
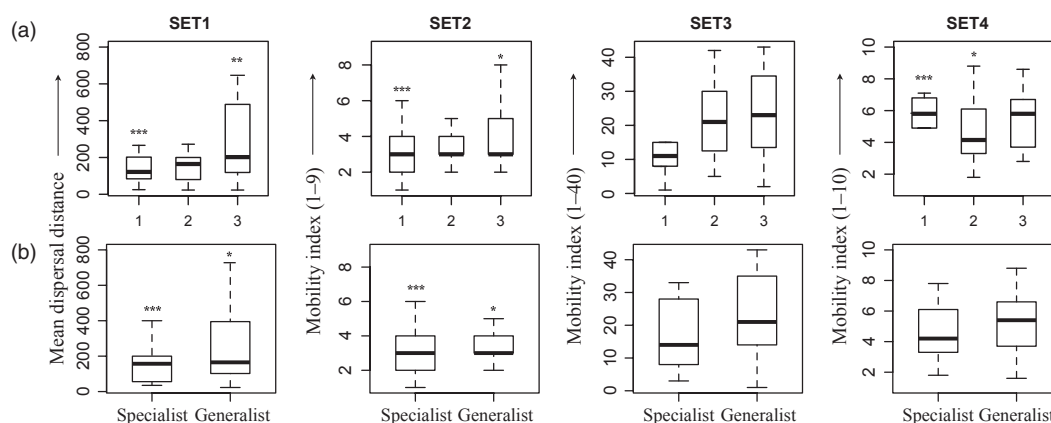


**Fig. 2.** Plot of dispersal ability with (a) larval host plant specificity and (b) adult habitat specificity for all data sets. Dispersal ability is mean distance dispersed (in metres) in SET1 and mobility index in the other data sets. SET2, 3 and 4 use different mobility indices. Significant results: '***' for $P < 0.001$; '**' for $P$ between 0.001 and 0.01; '*' for $P$ between 0.01 and 0.05. Larval host plant specificity has three levels: 1 – monophagous; 2 – oligophagous; and 3 – polyphagous larvae. Adult habitat specificity has two levels: specialist – adults restricted to a particular habitat and generalist – adults found in many habitats.
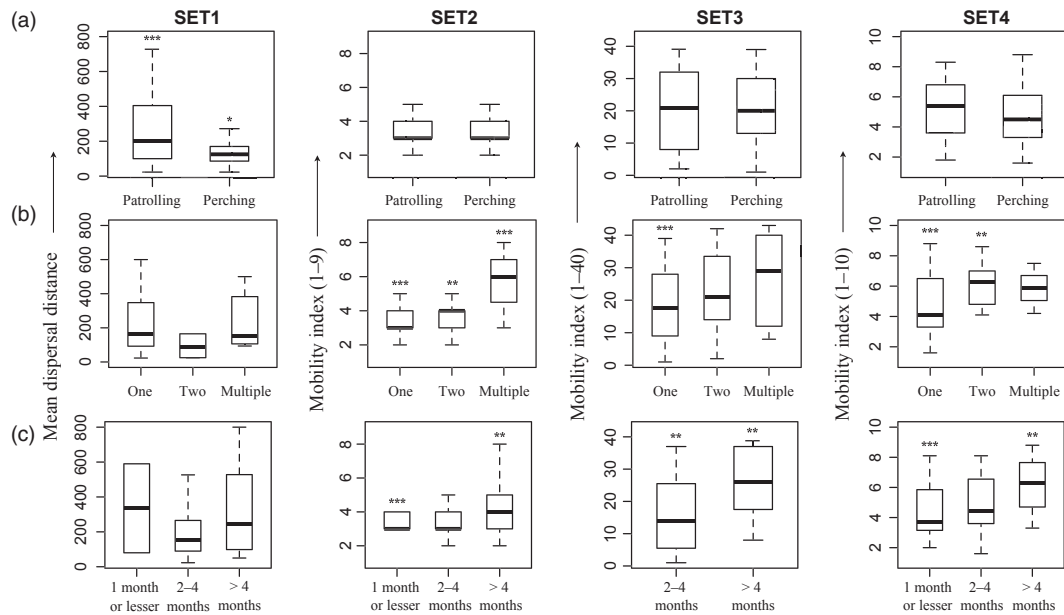
**Fig. 3.** Plot of dispersal ability with (a) mate location strategy (b) voltinism and (c) duration of flight for all data sets. Dispersal ability is mean distance dispersed (in metres) in SET1 and mobility index in the other data sets. SET2, 3 and 4 use different mobility indices. Significant results: '***' for $P < 0.001$; '**' for $P$ between 0.001 and 0.01; '*' for $P$ between 0.01 and 0.05. (a) Mate location strategy has two levels: patrolling and perching. (b) Voltinism has three levels: One: univoltine; Two: bivoltine; Multiple: multivoltine species. (c) Flight period duration also has three levels: 1 month or lesser, 2–4 months and more than 4 months.

mobility estimates. Also, the scoring adopted, which divided habitat specificity into just two classes, was probably too simplistic. A more rigorous analysis where habitat specificity is scored more informatively is needed (like in Koh, Sodhi & Brook 2004; Komonen *et al*. 2004). The kind of detailed information necessary for such scoring could not be obtained for this study.

Considering niche breadth as a whole, it seems like the patterns in a large-scale analysis like this one are driven by the species that are part of the data set and how the traits are scored. Also, some species that are specific to a particular biotope may fly large distances to locate their preferred habitat. But, it has also been shown that species with monophagous larvae occupy relatively small proportions of the area where their host is distributed, making it unlikely for host plant specialists to disperse more (Quinn *et al*. 1997). Spatial and temporal variabilities in host plant or habitat availability and intraspecific variations in the butterfly species can also interfere with the patterns that have emerged in this study (Burke, Fitzsimmons & Kerr 2011).

### MATE LOCATION STRATEGY

The effect of mate location strategy on dispersal ability is not strong in this study, as in case of previous studies. Butterflies that adopt perching as a strategy do not seem to disperse to a lesser extent than the species that patrol, except in case of SET1. Scott (1975) in a study of eleven species of butterflies showed that mate location strategy is important in determining difference in flight between males and females, but not differences between species. The effect is probably determined

by the nature of individual species in the data set, and the relationship between this factor and dispersal cannot be generalized without further examination. Moreover, mate location strategies can vary between populations of the same species because of local responses to fragmentation (Merckx & Van Dyck, 2005).

### VOLTINISM AND FLIGHT PERIOD DURATION

Voltinism affects dispersal ability in three data sets in the individual analyses and is retained in the MAM for SET2. Flight period duration is the second most important factor after wingspan, being an important predictor in three data sets in the unifactorial analyses and in two MAMs. This makes intuitive sense because SET2, SET3 and SET4, where the results are significant, predominantly consist of temperate species with varied numbers of generations; SET1 has a more heterogenous composition, with tropical and temperate species. Thus, temperate species that have more number of generations in a year, and which fly for longer periods once they emerge, are able to disperse to a greater extent. The positive effect of flight period length on dispersal ability has been demonstrated in the noctuid moths of Sweden (Betzholtz & Franzen 2011). Also, the length of the flight period of a butterfly species can reflect at least two things: the average life span of an individual or variance in the timing of hatching and consequent appearance on wing (Hodgson 1993). Adult life spans, in turn, have been suggested to affect dispersal abilities in flying insects, particularly over long distances (Beck & Kitching 2007 and the references therein).

MAKING INFERENCES ABOUT DISPERSAL ABILITY

In spite of the caveats regarding the data sets that have been discussed earlier, the use of multiple data sets allows for a meta-analytic approach to answer the question of which intrinsic traits affect dispersal ability in butterflies. Wingspan is clearly an important predictor, across all data sets. SET1 is different from other data sets because host plant specificity, habitat specificity and mate location strategy are significant in the unifactorial analyses, and only wingspan and host plant specificity predict dispersal ability in the MAM. In the other data sets, voltinism and flight period duration are the main predictors of dispersal ability (along with wingspan). This can be because of the nature of the data sets themselves. SET1 is composed of CMR studies from different places across Europe and North America, while the others are region-specific data sets that have been scored by experts. The results can represent an inherent bias in the results of the expert opinions, with species with greater wingspans and that are on the wing for longer periods of time being given a higher mobility score. The correlations between the predicted and observed dispersal ability (MDD or MI) checked after the MAMs were obtained show that the MAM for SET3 and SET4 are better predictors of MI. While SET1 has its own set of assumptions that has already been discussed, SET2 has a very low correlation, probably because it consists of mobility ranks from one source. The model for SET3 predicts MI best.

Nevertheless, using multiple data sets and several statistical tools to control for biases, the study provides insight into the intrinsic species traits that affect dispersal ability. These traits assume greater importance in that they can potentially affect other processes related to dispersal ability, like species distribution, range size, colonization ability and extinction proneness. Larval diet breadth and adult habitat specialization are seen to affect distribution of butterfly species, with specialist butterflies having smaller distributions (Päivinen *et al.* 2005). Migration to new habitats is greater in organisms with larger wingspans and wider dispersal capabilities, especially for those species whose opportunities are extended by a longer adult life span, longer flight period and multiple broods in any year (Dennis *et al.* 2000). Similarly, opportunities for colonization would be greater in species with abundant host plants, and occupy a wide range of habitats.

The factors affecting dispersal ability are also seen to affect extinction proneness in tropical butterflies (Koh, Sodhi & Brook 2004). Kotiaho *et al.* (2005) in an analysis of ecological characteristics of threatened and nonthreatened butterfly species in Finland, showing that threatened butterflies are characterized by narrow niche breadth, restricted resource distribution, poor dispersal ability and short flight period. Öckinger *et al.* (2010) showed that species with low mobility, a narrow feeding niche and low reproduction were most strongly affected by habitat loss; this is illustrated by the higher rate of decline among specialist butterflies of grassland (*c.* 19%), wetlands (*c.* 15%) and forests (*c.* 14%), than habitat generalist species (*c.* 1%) (van Swaay, Warren & Loïs 2006).

The results suggest that wingspan is the most important predictor of butterfly dispersal ability, followed by flight period duration in the case of temperate species. Using wingspan as the only proxy for dispersal ability maybe problematic because of the poor predictive power of the regressions. But, the tight relationship between wingspan and dispersal ability, as shown by the high degree of correlations in all data sets (effect size measurements), makes it a satisfactory proxy when no other information is available, especially for large-scale analyses. The importance of dispersal ability as a key intrinsic trait determining the ability of a species to survive in a hostile environment cannot be overemphasized, especially in view of the high degree of habitat loss and fragmentation all over the world today. Butterflies are an excellent model system to monitor species response to fragmentation pressures, being very sensitive to ecosystem changes. The high variability among studies trying to link intrinsic species-specific traits to dispersal makes a synthesized meta-analysis such as this important.

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## Supporting Information

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

**Appendix S1.** Datasets used in the paper.

**Appendix S2.** The phylogenetic trees used for the phylogenetic generalized least squares analysis.

**Appendix S3.** Results for the linear models for all datasets.

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