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Research

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Ranking the ecological causes of dispersal in a butterfly

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Dispersal, i.e. movements potentially leading to gene flow, is central in evolutionary ecology. Many factors can trigger dispersal, all linked to the social and/or the environmental context. Moreover, it is now widely demonstrated that phenotypes with contrasted dispersal abilities coexist within populations of a same species. The current challenge is to elucidate how social and environmental factors will influence the dispersal decision of individuals with distinct phenotypes. We have used the Metatron, a unique experimental mesocosm dedicated to the study of dispersal within fragmented landscapes, to analyze the relative and interactive roles played by ten potential dispersal triggers in experimental two-patch metapopulations of butterflies. We demonstrate in our model species that some factors (flight performance and wing length) have direct effects on emigration decision, others act only through interactive effects (sex ratio), while a third class of factors presents both direct and interactive effects (weather conditions, habitat quality and sex). We also show that disperser and resident individuals have distinct behavioral and morphological attributes, revealing the existence of a dispersal syndrome. Finally, our results also suggest that the environmental context, and especially weather conditions and habitat quality, prevails over social factors and individual phenotypes in butterflies' decision to disperse. Our approach is applicable to many species facing medium to strong environmental fluctuations, and constitutes a new way to master the idiosyncrasy of the dispersal process. Our framework should also help prioritize the factors responsible for populations' spatial distribution, which is obviously crucial in the current era of global changes.

The response of species to environmental changes is a subtle blend of three ingredients: tolerate new conditions or adapt to it, move to escape it, or decline locally. Dispersal, the movement of individuals potentially resulting in gene flow between local populations (Ronce 2007) is key in all these ingredients: it has a considerable role in the evolution of local adaptations (Doebeli and Dieckmann 2003), in the colonization of new areas to track suitable environmental conditions (Parmesan and Yohe 2003), and in the rescue of declining populations or in the recolonization of empty habitats after local extinction (Hanski 1999). Reliable predictions of the potential for evolutionary adaptations, of distribution shifts under changing environmental conditions, or of metapopulation dynamics require thus accurate information on dispersal (Kokko and López Sepulcre 2006, Clobert et al. 2012). However, most models aiming at predicting species' distribution under different scenarios of environmental changes are currently limited by a lack of, or incomplete treatment of dispersal due to its inherent complexity (Travis et al. 2013).

Because dispersal has multiple functions and involves many different mechanisms, therefore, it is likely to be driven by a combination of individual characteristics and environmental effects (Bowler and Benton 2005, Matthysen 2012). Over the last decades, many experimental studies confirmed the multicausality of the dispersal process across many taxa (Nunes et al. 1999, Forero et al. 2002, Massot et al. 2002, Delgado et al. 2010, reviewed by Matthysen 2012). From this accumulation of knowledge on dispersal causes, it has progressively begun obvious that it is the interaction between the individual phenotype and the particular social and environmental contexts that will influence why, when and where individuals disperse. In addition, recent reviews pointed that these multiple dispersal causes are susceptible to act interactively on each of the three steps of the dispersal process, i.e. emigration, transfer and settlement (Clobert et al. 2009, Bonte et al. 2012, Matthysen 2012), which means that dispersal is most often unpredictable in space and time (Bowler and Benton 2005).

At the interspecific level, several general rules linking dispersal rates and distances to particular life history traits have been evidenced (Stevens et al. 2012, 2013, 2014). At the intra-specific level, there have been few attempts to determine how dispersal causes interact (see however Donohue 1999, Bonte et al. 2008), and the potential hierarchy of environmental, social and phenotypic factors influencing the dispersal decision remains still unknown. We are aware of only one theoretical model suggesting that environmental factors are more important than social factors (Gandon and Michalakis 2001), but this model do not integrate the phenotypic variation in dispersal. However, theory suggests, and experimental studies confirm that dispersal distances vary according to the dispersal cause and the disperser phenotype (Clobert et al. 2008, 2009, Bitume et al. 2013, Duputié and Massol 2013). The identification of which factors are the primary drivers of dispersal can therefore substantially improve the precision of dispersal rate and distance predictions.

Here we tackle this challenge with an original approach: we used a combination of experiment and statistical modeling to disentangle the relative effects of ten distinct dispersal triggers on the decision to emigrate (i.e. the first step of the dispersal process) in a butterfly. Our main aim was to test the validity of two hypotheses 1) dispersal drivers can have both additive and interactive effects on emigration, and 2) some dispersal drivers are more important than others in emigration decision, i.e. it will thus be possible to rank the dispersal causes. The evolutionary ecology of dispersal has long been studied on butterflies and has generated many novel insights (Hanski et al. 2006, Schtickzelle et al. 2006, Stevens et al. 2010). Among butterfly model species, the large white butterfly *Pieris brassicae* shows a natural variability in behavioral, physiological and morphological traits that are associated into a mobility syndrome (Ducatez et al. 2012a, b, Larranaga et al. 2013). Some of these traits are dependent upon landscape properties and this relationship varies with sex (Ducatez et al. 2012a), which means that mobility is context- and condition-dependent in this species.

Material and methods

Butterfly breeding and characterization of phenotypic traits

In summer 2010, we collected 41 *P. brassicae* clutches originating from two 20 km-distant sites in Ariège (France) and reared the caterpillars hatching from each clutch in separate plastic boxes. Boxes were placed in climatic chambers at 23°C ± 1°C under controlled photoperiod conditions (light:dark, 14:10 h) mimicking favorable season conditions (from April to November in *P. brassicae*) that allow continuous development. Fresh cabbage was provided ad libitum to caterpillars. These individuals were then kept in the lab under common garden conditions similar to those of caterpillars (23°C ± 1°C and light:dark, 14:10 h) and fed with fresh flowers.

We studied five phenotypic traits linked to dispersal (Hanski et al. 2006, Bonte and Saastamoinen 2012, Ducatez et al. 2012a, Sekar 2012) and related to morphology, physiology, and behavior in 212 butterflies. Individuals were all marked with a specific number on their wings and sexed after they were completely dry. One day after emergence, we measured the following individual parameters: – wing length: one experimenter measured the left forewing length of each individual using a caliper (measures of the two wings are highly correlated in *P. brassicae*, Larranaga et al. 2013, Chaput-Bardy et al. 2014). – Flight performance: butterflies were tested with a previously described flight performance test (Ducatez et al. 2012b, c) Briefly, each individual was placed in a 25 × 10 × 10-cm plastic chamber, which was perforated at its base and fixed to a rapid agitator (Vortex Genie 2, Scientific Industries). Experiments were performed at 23 ± 1°C, which is considered as the optimal temperature for *P. brassicae* (Feltwell 1982). After a one-minute habituation period, the vortex was used to strongly shake the chamber, impeding the butterfly from perching on the walls. The butterfly's behavior was then observed for a period of one minute. During the test, the butterflies either took flight or rested uncomfortably at the bottom of the agitating chamber. The time an individual spent flying was then recorded, with high values reflecting good flight performance. – Thermoregulation ability: we measured the heating rate of butterflies based on a previously reported protocol (Ducatez et al. 2012a). Each individual was first cooled in a refrigerator (4°C, 10 min) and then warmed at 27°C for 180 s under a 300-W Ultra Vitalux solar lamp placed at a distance of 80 cm. During this warming procedure, the thorax temperature was monitored continuously with a TESTO845® infrared thermometer (emissivity $\varepsilon = 0.95$, one data point s^{-1} for 180 s). Heating rate was expressed as the slope of the thorax temperature plot versus the log-transformed time (Van Dyck and Matthysen 1998).

Finally, we determined the age of each individual at the beginning of the dispersal experiment. This was important because the emergence of butterflies was asynchronous, and they were kept in the lab until a sufficient number of individuals were available to perform the first release session in the Metatron.

Experimental design and determination of habitat characteristics

Previously we designed the Metatron (Fig. 1a), a unique experimental platform dedicated to the study of dispersal in terrestrial organisms that allows the manipulation of both spatial and climatic effects (Legrand et al. 2012). The use of the large white butterfly as a model system in the Metatron has been formerly validated (Legrand et al. 2012). We utilized 16 cages of the Metatron (each 200 m^3, 10 × 10 × 2 m and covered with insect-proof nets) experiencing different weather and habitat quality conditions, which allowed the creation of eight simple, two-patch metapopulations of butterflies living within natural environmental gradients (Fig. 1a, b, c). We connected each departure cage (in which butterflies were released) to an arrival cage using a corridor. Thus, the butterflies could either remain in the departure cage or freely cross a corridor into the arrival cage, with the possibility of returns to the departure cage. However, the narrow, S-shaped 19-m long corridors were designed to

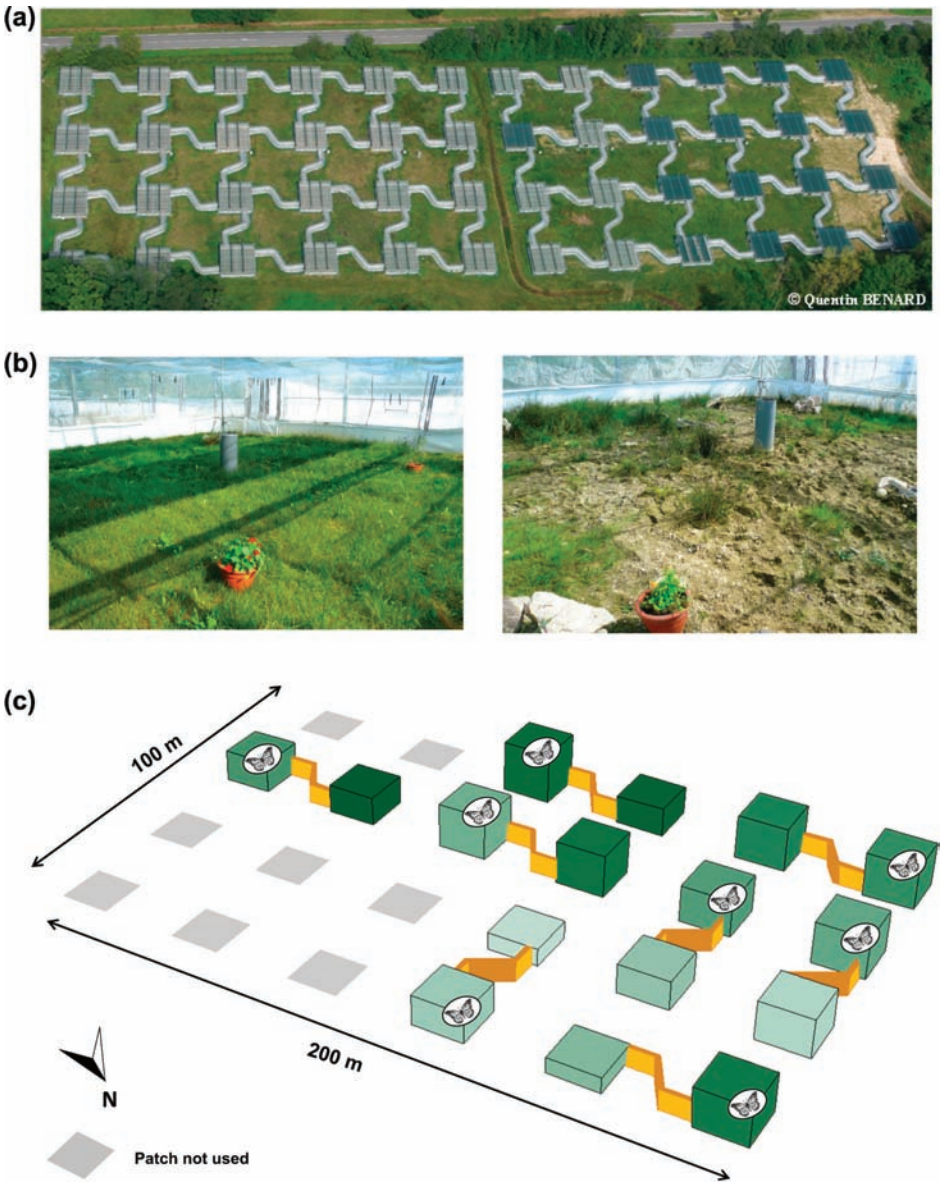

Figure 1. (a) Aerial photograph of the Metatron. The basic units of the Metatron are cages of 10 × 10 m, 2 m height fenced by tarps near the ground and a solid entomological net above, with herbaceous vegetation mowed twice a year. Cages are connected by 19 m, S-shaped narrow corridors. The present experiment was performed on the left hand cages of the photograph. (b) Photographs of a butterfly high-quality (dense vegetation cover) and a low-quality (sparse vegetation cover) cage. (c) 3D representation of the experimental design. We released 120 butterflies into eight departure cages (butterfly pictures on the scheme), each connected to an initially empty arrival cage.

be particularly challenging to cross (i.e. entries represented less than 2% of the total vertical surface of a cage fence) in order to allow discrimination between dispersal and resident individuals (Legrand et al. 2012). We also cut the vegetation to a very low height (i.e. without feeding flowers), ensuring unfavorable life conditions in the corridors. Within each departure and arrival cage, we placed feeding flowerpots and host plant pots in the same positions. We have previously shown that these conditions allowed the discrimination of dispersal events in *P. brassicae* (Trochet et al. 2013). In this study, we had introduced highly mobile butterflies within a similar two-patch configuration and identical corridor vegetation treatments, and we had observed that changes in population sex-ratio changed the dispersal decision of individuals.

In the present study, we recorded weather conditions by monitoring temperature, humidity, and luminosity via probes at the center of each cage every ten minutes throughout the experiment (Schneider Electric, SHO100 for temperature and humidity, precision = ± 0.4°C and 3% respectively; SLO310, precision = ± 5% for luminosity). We excluded data recorded during nighttime because *P. brassicae* is inactive under dark conditions. These recordings were averaged between successive capture sessions (between $t - 1$ and t) to summarize weather conditions during each time interval. The three variables were then summarized by a principal component analysis (PCA, Supplementary material Appendix 1), as they were highly correlated. Within each cage, weather conditions were thus described by their scores along the first axis of the PCA (hereafter PCA1) for

those with eigenvalues > 1.0. These variables accounted for 83.13% of the total inertia of the weather factors.

We determined the habitat quality within both the departure and arrival cages using a standardized protocol for vegetation sampling. We delimited 100 squares (1 m² each) on the ground of each of the 100 m² cages and photographed the individual square from a height of 1.50 m. This method allowed sufficient resolution for the identification of all plant species within these squares. Using ArGis 9.3 software, each of the 1600 resulting pictures (100 squares, 16 cages) were geolocated to recreate a composite surface image for each cage. We computed first two simple indexes of vegetation: – cover rate is the proportion of vegetal covering of the ground surfaces of the cages (Fig. 1b, c); – floristic richness is the total number of species within a cage (Fig. 1b).

We then used the list of plant species and their relative positions in each cage to delineate plant communities. A community is defined as the smallest group of ecologically similar species colonizing an area and growing together within the same strata during the same period. We used Phytobase 8 (Gillet 2010) to cluster species in communities on the basis of the recurrent association of plant species according to their ecological requirements. The resulting 6 communities and their species composition are described in the Supplementary material Appendix 1. We then computed for each cage its: – vegetal community diversity by using Shannon diversity index (N') applied to phytosociology:

$$N_q' = \exp\left(-\sum_{i=1}^{q} S_i \ln\left(S_i\right)\right)$$

where S_i is the relative abundance of community i and q is the total number of communities within cage s. – Number of vegetal communities, i.e. the number of statistically homogenous groups of species (vegetal community, see above). Adults of *P. brassicae* use a large panel of nectariferous flowers and hide on ground vegetation (Feltwell 1982). The higher values of these four indexes will be, the greater habitat quality will be considered.

These habitat quality variables were highly correlated and were thus summarized using two other PCAs: one for departure cages (PCA2) and one for arrival cages (PCA3). Habitat quality for each cage was described using its score along the first axes of these PCAs for eigenvalues > 1.0, accounting for 83.91% (PCA2) and 74.09% (PCA3) of the total inertia of the habitat quality variables in the departure and arrival cages, respectively (Supplementary material Appendix 1).

Capture–mark–recapture sessions and population structures

We initially introduced 120 butterflies, which were randomly chosen among 41 clutches, into the eight departure cages. Four of the populations consisted of 20 butterflies, whereas the other four populations were comprised of 10 butterflies. These eight populations had balanced sex ratios at the beginning of the experiment. We subsequently performed capture sessions twice a day under good meteorological conditions (i.e. no captures on rainy days) in order to record the position of each individual until death (i.e. departure cage, corridor, or arrival cage). To maintain sufficient population densities, we replaced dead butterflies with individuals emerging from our stock of clutches for as long as possible (92 more butterflies, thus a total of 212 individuals was released during the experiment). In total, 29 capture sessions were conducted during the 28 d of the experiment, i.e. until all butterflies died. During the four extra release sessions we introduced 35, 29, 9, and 19 butterflies. The lifetime capture histories of the butterflies were analyzed within the capture–mark–recapture framework (Lebreton et al. 1992). We calculated the catchability, the number of individuals of each sex in each capture session, and the survival probability between capture sessions. These values were determined for the pairs of cages as well as for departure cages, employing the POPAN model using Mark software (White and Burnham 1999). We included sex, flight performance and time as covariables, and we averaged the parameters of the best models (those for which the ΔAIC values were < 2) using the RMark package (Laake 2013). The daily survival rate and catchability were high and equivalent for all pairs of cages (on average: 0.8 and 0.83 for females, respectively, and 0.7 and 0.81 for males, respectively), which indicated that data from all replicates were informative. The POPAN results were used to determine departure cage population structures just before each emigration event. Sex ratio described the ratio of the number of males to females, whereas population density was considered to be the total number of individuals alive in cage s at time t.

Ranking of dispersal causes

The modelling procedure to rank the studied dispersal causes was performed in three steps.

Model 1: to study the effects of environmental and social factors on dispersal, we defined dispersal as a binomial: dispersal or residency events, i.e. a specific event within the individual history of each butterfly. To do this, we extracted the capture histories for each individual at the end of the CMR sessions and separated them into two categories: a residency event corresponded to the capture of an individual in the same cage (departure or arrival) at time $t-1$ and t, and a dispersal event corresponded to the capture of an individual in a different cage between time t and $t-1$. Movements from the departure to the arrival patches and returns were treated as independent dispersal events. We excluded the events at time t for which butterflies had not been recaptured at $t-1$ because we could not ascertain whether these events occurred during the preceding time interval. We determined the environmental conditions for each dispersal event at time $t-1$ and recorded these values as explanatory variables, except for weather conditions that were averaged between t and $t-1$. To evaluate the effects of the five environmental factors on residency or dispersal events, we ran generalized linear mixed-effect models (GLMMs) using the lme4 package (Bates et al. 2008) in R 2.14.2 (R Core Team). Population density, sex ratio, weather conditions (summarized by the

coordinates on the first axis of PCA1), habitat quality at departure (summarized by the coordinates on the first axis of PCA2), and habitat quality at arrival (summarized by the coordinates on the first axis of PCA3) were used as variables with fixed effects. Pairs of cages and individuals nested in their clutch of origin were included as factors with random intercepts. A full model that included all first-order interactions would have been overparameterized. Therefore, we refined the variable selection by starting with five different full models in which we retained all single effects, analyzing the interactions between one variable with all others. This selection process allowed us to retain the interaction effects that returned the lowest AIC values in a single model. We then compared the models nested within the full model to select the combination(s) of terms that returned the best AIC. We employed a model averaging procedure to determine the relative importance of each factor. The best models (i.e. those with ΔAIC values < 2) were averaged using the MuMIn package (Bárton 2013). Two elements derived from this averaging procedure were used to assess the importance of each factor in butterfly dispersal: 1) the confidence interval of the averaged estimated slope of the selected term (i.e. strong effects had confidence intervals that did not contain zero, marginal effects were those with confidence intervals containing zero and shifted toward positive or negative values, negligible effects displayed confidence intervals roughly centered on zero); 2) the relative weight of the term (i.e. the relative sum of Akaike's weights of the models, within the subset of models with ΔAIC < 2 in which the term was included).

Model 2: to study the effects of phenotypic traits on dispersal, we used a binomial variable describing the dispersal status of each individual, i.e. the general 'dispersotype' of an individual. We considered dispersers to be the butterflies that were captured either in a corridor or an arrival cage at least once, while residents were butterflies that stayed within departure cages throughout their lifetimes. Individuals that were never recaptured after their release ($n = 42$ over the 212 released butterflies) were not included in the analyses. We ran GLMMs using sex, age, flight performance, wing length, and thermoregulation ability as variables with fixed effects, whereas the pairs of cages and the individual's clutch of origin were included as factors with random intercepts. The same approach as in model 1 was used to determine the additive and interactive effects of each tested variable.

Model 3: we built a third model to compare the relative weight of phenotypic traits and environmental factors in the dispersal decision. This model included factors that had a relative importance > 0.5 in models 1 and 2 after model selection. Dispersal events were set as the response variable (environmental factors, as measured in our experiment, were not appropriate for use in models with the dispersal status as the response variable because the dispersal status is fixed over individual lifetime while environmental factors vary), with the pair of cages and the individual's identity nested in its clutch of origin as factors with random intercepts. The same approach as in model 1 was used to determine the additive and interactive effects of each tested variable.

Before running the three models, we verified that the variance inflation factor was < 2 for all explanatory variables, using the car library in R (Fox and Weisberg 2011), meaning that there was no multicollinearity among them. We also verified with a separate model that the orientation of the corridors had no effect on dispersal. Finally, we verified that each variable included in PCAs had individual effects corresponding to results obtained when models were run with summarized data. To do so, we ran successive models including only one of the variables summarized in each PCA (all combinations were tested) because full models were over-parameterized. As results were always concordant, we present models with PCAs in the Results section to gain in clarity, but we rather use individual variables in the Discussion section to simplify the interpretation of the data.

Results

We recorded 46 dispersers and 124 residents; this means that 27% of individuals were dispersers. In total, 77 dispersal events, including 26 returns, and 717 residency events were documented in the capture history of individuals. We then ran our three models to determine the relative importance of environmental context and individual phenotypes on emigration decisions.

Effects of environmental and social factors on emigration

Model 1 shows that weather conditions and habitat quality at departure had the strongest effect on emigration (Table 1). Emigration was positively related to daily air temperatures (Fig. 2a) and luminosity, and negatively related to humidity. Moreover, results indicate that low-quality departure cages (i.e. low floristic richness and sparse vegetal cover, Fig. 2b) encouraged dispersal. Individuals were also marginally encouraged to disperse by high-quality arrival cages. Marginal interactive effects between weather conditions and habitat quality of the departure and arrival cages were observed. Indeed, extreme air temperature led to increased emigration regardless of the cages' quality.

Interestingly, social factors were not important in emigration decisions. Indeed, population density was not retained in the best models and population sex ratio was kept only through a strong interaction with weather conditions. Under moderate temperatures, we observed a general increase in emigration rate when a greater proportion of males was present. However, as air temperature increased and humidity decreased, emigration was independent of population sex ratio.

Effects of phenotypes on emigration

Model 2 shows that sex had the strongest effect on emigration rate with a dispersal biased toward females (Table 1, Fig. 3a). While age and thermoregulation ability had no effect on emigration, both the wing length and the flight performance had a significant effect ($p < 0.01$ and $p < 0.001$ respectively, Wilcoxon t-test; Fig. 3b, c).

Table 1. Ranking of dispersal causes.

Model terms			Estimate	95% CI of estimate	Weight
		intercept	–3.91	–4.64; –3.18	
Model 1: environmental factors and their interactions	Simple terms	weather	0.82 ***	0.35; 1.26	1
		habitat quality at departure	–0.75 *	–1.45; –0.05	1
		population sex ratio	0.5	–0.30; 1.29	1
		habitat quality at arrival	0.45	–0.25; 1.16	0.72
		population density	not retained by selection		
	Interaction terms	weather:sex ratio	–0.53 *	–0.97; –0.09	1
		weather:habitat quality at departure	0.2	–0.18; 0.59	0.42
		weather:habitat quality at arrival	0.25	–0.18; 0.69	0.33
		other interactions	not retained by selection		
		intercept	–0.71	–1.39; –0.03	
Model 2: phenotypic traits and their interactions	Simple terms	sex	–1.02 ***	–1.81; –0.22	1
		flight performance	0.28	–0.14; 0.69	0.45
		wing length	0.25	–0.15; 0.65	0.42
		age	not retained by selection		
		thermoregulation ability	not retained by selection		
	Interaction terms	all 2-ways interactions	not retained by selection		
		intercept	–3.75	–4.57; –2.93	
Model 3: environmental vs phenotype and their interactions	Simple terms	weather	0.79***	0.33; 1.25	1
		habitat quality at departure	–0.56	–1.23; 0.12	1
		population sex ratio	0.83	–0.09; 1.75	1
		sex	–0.1	–1.40; 1.21	0.89
		habitat quality at arrival	0.33	–0.42; 1.08	0.67
	Interaction terms	weather:sex-ratio	–0.68**	–1.11; –0.24	1
		sex:population sex-ratio	–1.31*	–2.56; –0.06	0.77
		sex:habitat quality at departure	–0.87	–2.36; 0.63	0.43
		sex:weather	–0.49	–1.32; 0.34	0.33
		sex:habitat quality at arrival	0.83	–0.49; 2.16	0.28

We used linear mixed-effect models to select environmental factors (model 1) and phenotypic traits (model 2) that best predict dispersal decisions. A full model incorporating all of the factors from both categories would have been overparameterized. Therefore, factors with the strongest effects in models 1 and 2 (i.e. those with weights > 0.5) were selected for inclusion in model 3, which compared the relative importance of environmental and phenotypic traits in the dispersal decision. A dispersal or residency event (extracted from capture histories of individuals) was used as response variable in model 1 and 3, and the dispersal status of individuals (resident or disperser) was used as response variable in model 2. Weights = relative Akaike weight of the top-ranked models ($\Delta AIC < 2$) in which the term appeared. *** = $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Weather conditions and habitat quality are quantified using PCAs (see Material and methods and Supplementary material Appendix 1).

More mobile individuals as well as individuals with longer wings were more prone to leave the departure cage. Finally, we did not find evidence of significant interactive effects among phenotypic traits.

Preeminence of environmental factors over phenotypes

Model 3 included all significant effects retained in models 1 and 2. Weather conditions and habitat quality at departure had the strongest impact on emigration. Population sex ratio was kept only through the same interaction as described in model 1 with weather conditions. All other interactions retained by selection had marginal effects and included sex, which is the only phenotypic trait that was kept in model 3. The tendency to emigrate from a cage with a higher proportion of males was stronger for females, which were also more sensitive to warmer conditions than were males. However males were more sensitive to the quality of both departure and arrival cages, because they leaved more often poor-quality departure cages and avoided more often poor-quality arrival cages than females.

Discussion

Dispersal evolved as a common solution to multiple problems. Although numerous studies have demonstrated that the environmental and social context together with the phenotype of the individual concur to trigger dispersal, both in nature and under fully controlled conditions (Lens et al. 2002, Ferraz et al. 2007, Bonte et al. 2008), multifactorial tests of the interactive and relative role of each of these factors are still lacking (Bonte et al. 2012, Matthysen 2012). This is mainly because it is technically difficult to control for more than a few factors under natural conditions (Haddad 2012, Legrand et al. 2012). The pros and cons of the Metatron in studying dispersal have been lengthy discussed elsewhere; to sum up, this mesocosm provides an unrivaled opportunity to experimentally test the decision an individual will take to emigrate or not, which is the first step of the dispersal process

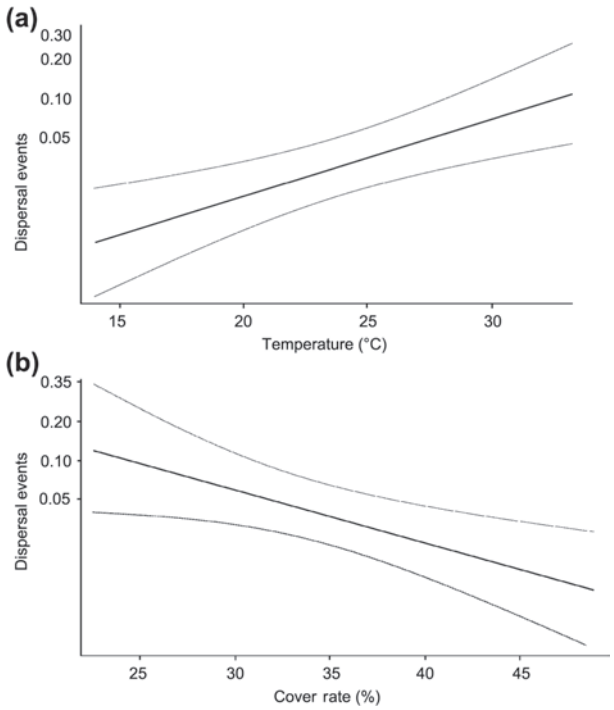

Figure 2. (a) Plot displaying the proportion of emigration events as a function of the temperature in the best-fitted model. (b) Plot displaying the proportion of emigration events as a function of vegetal cover in departure cages in the best-fitted model.

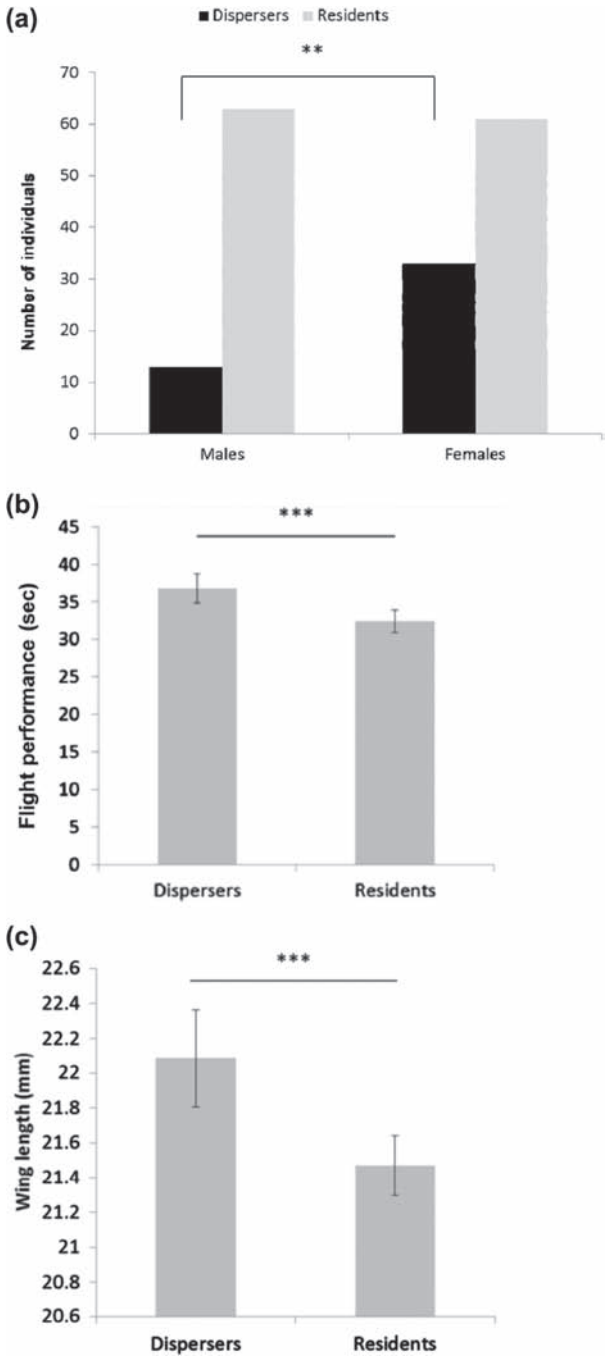

Figure 3. (a) Dispersers and residents were quantified based on sex. The data indicate a significant female-biased emigration ($p < 0.01$, Wilcoxon t-test). (b) Average flight performance (and standard error) of dispersers and residents ($p < 0.001$, Wilcoxon t-test). (c) Average wing length (and standard error) of dispersers and residents ($p < 0.001$, Wilcoxon t-test).

(Haddad 2012, Legrand et al. 2012). Using the Metatron, we provide here the first ranking of ten different dispersal factors on a Metazoa at a previously unexplored spatial scale.

Weather conditions and habitat quality had the strongest impact on individual emigration decisions. Butterflies were more prone to emigrate from the departure cage when air temperatures were high and presumably far from optimal (*P. brassicae* distribution is limited southward by the summer isotherm of 28°C, Feltwell 1982), whereas high humidity rates impeded dispersal. In relation to their lifestyle, butterflies were directly encouraged to emigrate from low quality cages, i.e. from those with the lowest vegetal cover and species richness. *Pieris brassicae* (Feltwell 1982) and numerous butterfly species (reviewed by Erhardt and Mevi-Schütz 2009) indeed feed on a large panel of nectariferous flowers and hide on ground vegetation. Habitat quality in arrival cages had a marginal, yet important, role in dispersal (immigration was higher in arrival cages of better quality). Information about arrival cages might be provided by round trip after initial visits to low quality arrival cages, or by the acquisition of information about distant cages using olfaction or social interactions (Cote and Clobert 2007, Baguette et al. 2011). Interestingly, our results corroborate previous observational and correlation data documenting the importance of weather conditions and habitat quality on the emigration decision in butterflies (Conradt et al. 2001, Cormont et al. 2011, Krämer et al. 2012), which confirms the accuracy of our system to study dispersal in butterflies (Legrand et al. 2012).

About social factors, population density was not retained in the model, and population sex ratio was only kept through a strong interaction with weather factors. Contrary to our results, several studies documented strong density-dependence of emigration in butterflies (reviewed by Hovestadt and Nieminen 2009), either positive (Enjfäll and Leimar 2005, Nowicki and Vrabec 2011) or negative (Kuussaari et al. 1998, Roland et al. 2000). In the Metatron, individuals are confined in cages in which they may difficultly escape harassment and in which they probably suffer

from more physical injuries than in nature due to contacts with nets. Therefore, we used density levels situated at the lower end of the range compared to wild population densities reported in the literature for Pierid-related species (20 individuals 100 m^{-2} at maximum in our experimental metapopulations, 5–800 individuals 100 m^{-2} in nature, Shapiro 1970). To what extent higher densities would modulate emigration decision remains to be determined. Starting from equilibrated conditions, the sex-ratio changed according to the differential emigration of males and females. We report here increased emigration when a greater proportion of males was present, confirming our previous findings (Trochet et al. 2013). However, as for congener density, we did not explore the entire range of variation of sex-ratios, which can reach extreme values in butterflies, from almost 100% of males to 100% of females because of protandry (Schtickzelle et al. 2002) or Wolbachia infection (Dyson and Hurst 2004). Accordingly, the generalization of the prominent role of non-social versus social factors on the emigration decision requires complementary experiments.

Under our experimental conditions, butterflies were more sensitive to environmental than to social factors. The interactive effects between weather conditions and habitat quality on the one hand and between weather conditions and population sex ratio on the other hand (less important effect of departure cage quality and population sex ratio on emigration when temperatures were high) confirm the high sensitivity of butterflies to climate change (Warren et al. 2001, Breed et al. 2013). Under extreme temperature conditions, individuals will decide to disperse independently of other environmental cues.

Butterfly phenotypes strongly influenced their emigration decision. Sex had the strongest effect: like in many monoandrous butterflies, dispersal was female biased (Bonte and Saastamoinen 2012, Trochet et al. 2013) independently of the density of egg batches in the departure cage (data not shown). The avoidance of male harassment has been proposed as the main cause of female dispersal (Trochet et al. 2013), particularly in monoandrous species such as *P. brassicae*. Flight performance and wing length had significant effects on the emigration decision, good performers and individuals with long wings being more often dispersers. Flight performance is part of the mobility syndrome described for *P. brassicae* and is associated with both exploration skills and consistency of flight orientation after emergence (Ducatez et al. 2012b, Larranaga et al. 2013). Thus, given that flight performance as well as wing length are related to emigration decision, this mobility syndrome is now extended to a real dispersal syndrome, in which disperser and resident phenotypes have distinct behavioral and morphological attributes (Clobert et al. 2009). We observed no significant interactions between any of the phenotypic traits. This suggests that the dispersal syndrome of *P. brassicae* results from simple co-variations between traits, which raises interesting question about its genetic architecture. This dispersal syndrome in *P. brassicae* indicates that dispersers did not constitute a random fraction of the released individuals. This result implies that models aiming at predicting the dynamics of spatially-structured populations should integrate inter-individual variability in order to correctly capture the dispersal process.

Environmental factors were more influential than phenotypic traits during emigration decisions. It might be interesting to assess the fitness of those individuals that stayed in poor environmental conditions, those that emigrated because of phenotypic predisposition (i.e. context-independent dispersers), and those that emigrated in response to poor environmental conditions (i.e. context-dependent dispersers). Besides, our data also revealed the existence of marginal interactions between sex and four environmental factors, suggesting that males and females would respond differently to environmental changes.

To conclude, being context- and condition-dependent, dispersal is inherently an idiosyncratic process that will vary across organisms, space and time. Our study revealed that these multiple causes of dispersal have either simple or interactive effects on emigration, and that individuals are able to process information on environmental conditions according to their own phenotypic state to take the decision to leave a patch, i.e. to disperse. Because the Metatron can be used to study to a large panel of terrestrial and semi-terrestrial organisms (including plants, mollusks, arthropods, reptiles, amphibians), our approach has the potential to create a real breakthrough in dispersal research by providing the scientific community with the opportunity to experimentally test what are the main dispersal causes, and to determine how these cues are integrated by individuals in order to modulate their dispersal decision. Provided that complementary information of the dispersal process at larger scales are collected (for example through spatial genetic data), integrating such functional information in the recently developed modelling tools aiming at predicting species' responses to environmental changes (Bocedi et al. 2014) would offer a new manner to build integrated research programs in the context of global changes (Evans et al. 2013).

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DL, VS, JC and MB conceived the study. DL, AT and OC performed the experiment. All authors participated to the statistical analyses at the exception of CMR analyses that were performed by DL and SM. DL and MB wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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Supplementary material (Appendix ECOG-01283 at <www.ecography.org/readers/appendix>). Appendix 1.