

A meta-analysis of dispersal in butterflies

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(Received 11 June 2009; revised 02 December 2009; accepted 08 December 2009)

ABSTRACT

Dispersal has recently gained much attention because of its crucial role in the conservation and evolution of species facing major environmental changes such as habitat loss and fragmentation, climate change, and their interactions. Butterflies have long been recognized as ideal model systems for the study of dispersal and a huge amount of data on their ability to disperse has been collected under various conditions. However, no single 'best' method seems to exist leading to the co-occurrence of various approaches to study butterfly mobility, and therefore a high heterogeneity among data on dispersal across this group. Accordingly, we here reviewed the knowledge accumulated on dispersal and mobility in butterflies, to detect general patterns. This meta-analysis specifically addressed two questions. Firstly, do the various methods provide a congruent picture of how dispersal ability is distributed across species? Secondly, is dispersal species-specific? Five sources of data were analysed: multisite mark-recapture experiments, genetic studies, experimental assessments, expert opinions, and transect surveys. We accounted for potential biases due to variation in genetic markers, sample sizes, spatial scales or the level of habitat fragmentation. We showed that the various dispersal estimates generally converged, and that the relative dispersal ability of species could reliably be predicted from their relative vagrancy (records of butterflies outside their normal habitat). Expert opinions gave much less reliable estimates of realized dispersal but instead reflected migration propensity of butterflies. Within-species comparisons showed that genetic estimates were relatively invariable, while other dispersal estimates were highly variable. This latter point questions dispersal as a species-specific, invariant trait.

Key words: dispersal, mobility, vagrancy, migration, genetic structure, mark-release-recapture, Lepidoptera, butterfly, meta-analysis.

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I. INTRODUCTION

The biology of dispersal is fundamental to many areas of ecology and evolutionary biology, from issues of population regulation, through community dynamics, to gene flow and speciation (Clobert *et al.*, 2001; Bullock, Kenward & Hails, 2002; Bowler & Benton, 2005; Kokko & Lopez-Sepulcre, 2006). In addition, understanding dispersal is now of utmost importance in the context of habitat loss, fragmentation and global climate change. The ecological and evolutionary functioning of natural populations facing habitat fragmentation, shift of their climatic envelopes, or a combination of these, indeed relies on (1) the availability of functionally connected networks of habitats, and (2) that species have sufficient dispersal ability to track these dramatic changes. Dispersal also drives the spatial and temporal redistribution of genotypes that is inseparable from the evolution of life-history traits (Ronce, 2007).

Butterflies have long been recognized as ideal models for the study of fragmented populations because (1) for most species, their specialization makes their habitats relatively easy to map in heterogeneous landscapes (Baguette & Mennechez, 2004), and (2) the natural history of most species is well documented (e.g. Dennis, 1992; Ehrlich & Hanski, 2004; Dover & Settele, 2009; Boggs, 2009). They have also been used as models for studies focusing either on molecular adaptation leading to energetic optimization (Watt & Boggs, 2003), or on orientation processes (e.g. Rutowski, 2003). Hence butterflies have now been adopted as biological models in the integrated study of dispersal (Hanski & Kuussaari, 1995; Ehrlich & Hanski, 2004; Hovestadt & Nieminen, 2009) and several recent reviews report on butterfly dispersal in the context of climate change (Dennis, 1992; Parmesan *et al.*, 1999; Hill, Thomas & Huntley, 1999; Hill *et al.*, 2002; Nilsson, Franzen & Jonsson, 2008; Settele *et al.*, 2008; Poyry *et al.*, 2009), habitat fragmentation (Heikkinen *et al.*, 2005; Dover & Settele, 2009) and habitat deterioration (Ockinger *et al.*, 2006).

Ideally, to gain insights both on dispersal patterns and processes and on their evolution in an ever-changing environment, we should aim (1) to measure real-time flows of dispersing individuals in real landscapes, and (2) to have unlimited access to the identity, genotypes and motivation state of dispersing individuals, to their physiological and behavioural trade-offs, to their ability to collect and use information before and during the dispersal process, as well as to their relative fitness, which together will give us insights on gene flow patterns. Unfortunately, given the extreme technical difficulties, such data are often sporadic. To circumvent this drawback, a wide array of different methods is currently used to assess dispersal of individuals or species, giving a huge heterogeneity in dispersal data both at the inter-specific and the intra-specific levels.

Given the high levels of interest in this field, dispersal is probably documented best in butterflies over all other animal groups. Our aim herein is to explore whether a coherent picture of dispersal can emerge from the numerous

and heterogeneous data currently available on butterfly movement. More precisely, we attempt to (1) review the different methods of dispersal measurement in butterflies, (2) investigate how the heterogeneous movement data can provide consensual patterns of the organization of dispersal ability across butterfly species, and (3) assess within-species variation in dispersal.

We first present the assumptions made about dispersal inherent to each method of measurement. Next, we address specifically the generalization of the results at both inter-specific and intra-specific levels through a meta-analysis of the many studies addressing dispersal in European butterflies (Fig. 1). We have *a priori* decided to restrict our review to European butterflies. However, it should be relatively simple to apply the same methodology to other study systems.

II. HOW TO MEASURE BUTTERFLY DISPERSAL

Herein, we will refer to ‘dispersal’ for performances focusing explicitly on movements that potentially drive gene flow (see Table 1 for three different ways of considering dispersal), whereas we will use ‘mobility’ when considering other types of butterfly movement, including foraging movements, vagrancy or migration propensity. ‘Migration’ will only refer to directional and periodically reversed mass movements (even if these movements are not performed by the same individual). Dispersal studies are usually separated according to their methodology into direct and indirect investigations. Direct investigations include mark-release-recapture (MRR) or point-release experiments, the dynamics of patch colonization and extinctions, data on range expansions, occupancy of islands, or results obtained from cage experiments. Indirect methods rely on the description of the distribution of genetic diversity among local populations from which gene flow and inter-population genetic distances are inferred. Aside from dispersal measures, other butterfly mobility indices might be derived from expert opinion, from relative flight speed, and from records of vagrant individuals (butterflies recorded outside their habitats) or from migration behaviour. The parameters that are used to describe dispersal in butterflies are not interchangeable since they implicitly rely on different definitions of the process itself (see Table 1 and Appendix A).

Rather simple definitions of dispersal are based on processes acting on the individual (Table 1). For instance dispersal can be defined as the spreading of individuals away from each other (Begon, Townsend & Harper, 2006), or as the movement of an organism away from its birth place or from centres of population density (Ricklefs & Miller, 1999). The length of daily displacements corresponds to these individual-based definitions of dispersal because it is thought to reflect the relative ability of individuals (or when summed over individuals, that of populations or species) to spread away from their birth place. Range expansions and dispersal kernels—the probability density of recapture distances—inferred from MRR studies are also

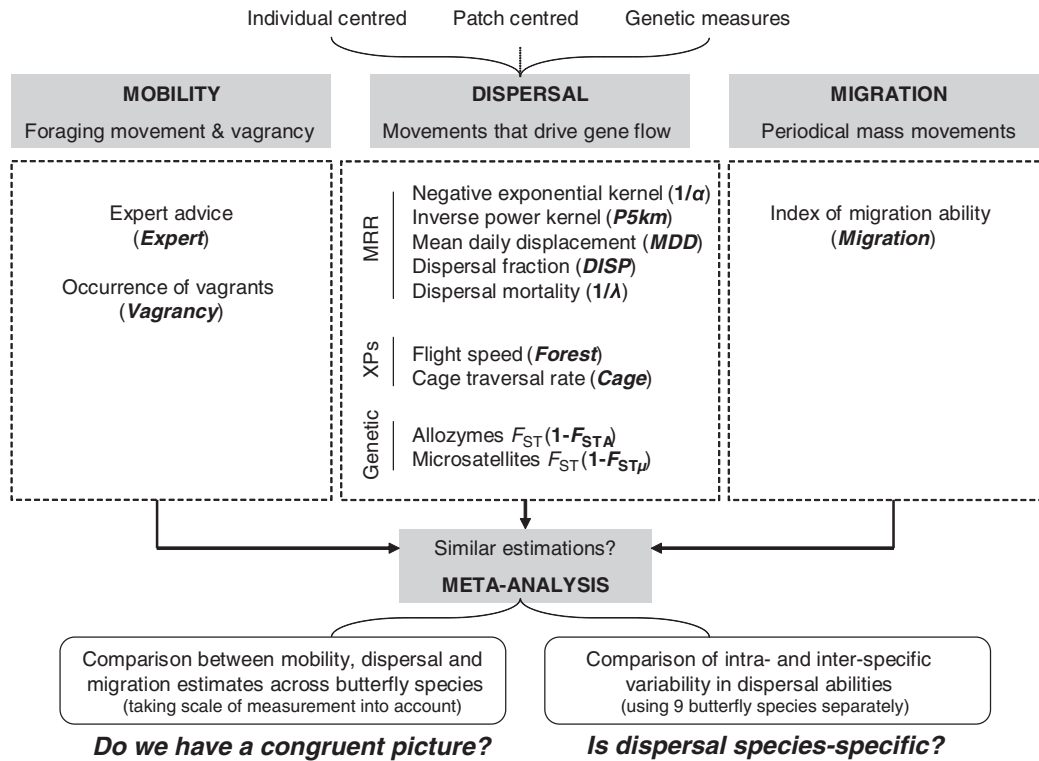


Fig. 1. Schematic representation of the meta-analysis on dispersal and mobility in butterflies. MRR = mark-release-recapture studies; XPs = experimental studies; F_{ST} = measure of genetic differentiation among populations: F_{STA} from allozymes, $F_{ST\mu}$ from microsatellites.

Table 1. Dispersal estimates used most frequently in butterfly studies and corresponding dispersal definitions

	Methods of butterfly dispersal measurement	Definitions of dispersal
Individual-centred definitions	Dispersal kernels Length of daily displacements Range expansions	Spreading of individuals away from others (Begon <i>et al.</i> , 2006). Movements of organisms away from their place of birth or from centres of population density (Ricklefs & Miller, 1999).
Patch-centred definition	Dispersal fraction Mortality during transfer Cage traversal Flight speed Patch occupancy	Departure from the current habitat patch (emigration), the seeking of a new patch, and the occupation of the first available and suitable habitat patch discovered (immigration) (Dingle, 1996).
Genotype-centred definition	Indirect methods (genetics)	The movement of an organism (or a propagule) that potentially may result in gene flow across space (Ronce, 2007).

based on individual movements. Dispersal kernels and range expansion data typically sum individual processes of moving from centres of population density, which are either local populations in the case of multisite MRR, or unidentified localities within the historical distribution range of species in the case of range expansion data. In our meta-analysis, we did not include range expansion data since they are not unequivocally linked to dispersal or mobility but are rather the result of the interaction between suitable environmental conditions, population dynamics, and individual mobility.

Other definitions of dispersal are patch-centred (Table 1). For instance, dispersal can be defined as departure from

the current habitat patch (emigration), the seeking of a new patch, and the occupation of the first suitable habitat patch discovered (immigration) (Stenseth & Lidicker, 1992; Dingle, 1996). This definition corresponds to dissection of the dispersal process into three behavioural components: departure, transfer and settlement (Ims & Yoccoz, 1997; Bowler & Benton, 2005; Baguette & Van Dyck, 2007; Clobert *et al.*, 2009), and obviously matches dispersal indices estimated from turnover in patch occupancy. This patch-based definition also fits some MRR-derived dispersal indices such as the dispersal fraction or the dispersal mortality. The dispersal fraction, i.e. the proportion of recaptures

in patches other than that of first capture, introduces a functional difference between movements of the same length depending on where they started and ended: in the same habitat patch (in which case the movement is not dispersal) or in different patches (where it is dispersal). Dispersal mortality may also serve as a tool to assess relative dispersal abilities of populations or species (Schtickzelle, Mennechez & Baguette, 2006). Undeniably, distinguishing those individuals that died during transfer from those that left the MRR study site is challenging, which hinders the assessment of dispersal mortality. However, some analytical advances have been made in multi-site MRR data analysis to solve this critical issue: for instance, the Virtual Migration model (Hanski, Alho & Moilanen, 2000) estimates the parameter λ that corresponds to the patch connectivity value at which half of the dispersers die during the transfer stage of dispersal. The experimental assessment of the rate of traversal of an unsuitable section of a cage is also intended to reflect the relative dispersal ability of individuals (Norberg, Enfjall & Leimar, 2002). Cage traversal studies also implicitly belong to the patch-based definition of dispersal, just as do some studies where the relative mobility of species is inferred from their flight speed in unsuitable habitats (for instance in Shreeve, 1981).

Finally, indirect investigations of dispersal are based on the genetic results of the process (Table 1). Dispersal is here considered as the movement of an organism (or a propagule) that results in gene flow across space (Ronce, 2007). We do not yet have convincing evidence that the amount of gene flow is proportional to the relative movement ability of a species (or population) as measured by direct methods. However, two studies that specifically compared the spatial structure of genetic diversity with the dispersal movements estimated by direct methods in the same landscape have shown that interpatch movement inferred from MRR studies truly and fully reflects dispersal in its genetic sense (Vandewoestijne & Baguette, 2004a; Vandewoestijne, Schtickzelle & Baguette, 2008).

III. DATA SELECTION FOR THE META-ANALYSIS

We investigated the generality of dispersal measures through a meta-analysis of published studies on mobility and dispersal in European butterfly species. To identify relevant empirical studies, we searched the Web of Science database[®] (1900-present) with various combinations of the following entries: (butterfly* or lepidopter*) and: (dispersal or dispersive or flight or migration or movement or vagran* or redistribution), (CMR or MRR or mark-release or mark-recapture), ([genetic* or allozym* or microsatellite* or RAPD or AFLP or SNP* or DNA] and [structure or population]), (landscape or metapopulation or fragmented population or range expansion or range shift). We also searched specifically for the co-occurrence of [dispersal or mobility or flight or genetic*] and [the name of each species] in the dataset. For

all identified citations, we selected the relevant studies on the basis of their titles and abstracts, and thoroughly searched for doublets (papers showing the same data) that were discarded (only one paper was retained). We included a few suitable data from unpublished material and from book chapters, or from papers that were identified from citations within papers found during the database search.

Using this procedure, we identified 99 papers reporting on butterfly mobility or dispersal ability (a complete list of references is given in Appendix A). We extracted from these papers nine dispersal estimates (seven direct and two indirect) and three measures of mobility, each available for more than five European butterfly species (see Table 2 and below for dispersal measures). Direct and indirect assessments of dispersal were available for more than 50 European butterfly species in total, and mobility indices are available for more than 140 species (Table 2).

(1) Dispersal data from multisite mark-release-recapture studies

Multisite MRR data were available for 35 species. From those, we extracted five dispersal indices: two types of dispersal kernels (negative exponential and inverse power functions, which are the most frequently used functions), the mean daily displacement, the dispersal fraction and the dispersal mortality.

First, we described the dispersal kernel—the inverse cumulative proportion of individuals moving certain distances—for 32 species. For all these species, the dispersal kernel can be fitted to a negative exponential function (SAS[®], proc NLIN, $P < 0.001$): $P(D) = e^{-\alpha D}$, where the probability to move a given distance [$P(D)$] is dependent on the distance (D) and the constant α , which is a synthetic descriptor of the kernel. Mean recapture distance decreased with increasing α , so we used $1/\alpha$ as an indicator of butterfly dispersal ability. $1/\alpha$ corresponds to the average distance (in km) moved by the butterflies. Metapopulation dynamics is known to be highly sensitive to the value of α in negative exponential dispersal kernels (Schtickzelle & Baguette, 2009).

For 30 of those species, we were able to fit the kernel (SAS[®], proc NLIN, $P < 0.001$) to an inverse-power function of the form: $P(D) = aD^{-b}$. Inverse power functions generally give a better fit to long-distance movements than do negative exponentials (Hill, Thomas & Lewis, 1996; Baguette, Petit & Quéva, 2000; Baguette, 2003; Fric & Konvicka, 2007). Hence, we summarized inverse-power kernels using the predicted relative frequency of moves equal or exceeding 5 km ($P5km$).

The shape of the negative exponential kernels ($1/\alpha$) was highly sensitive to the spatial extent of the study site (Table 3, model 1). We therefore grouped MRR studies into two spatial scales: large units (when the longest length of the study site was more than 1.9 km, the median length in our dataset), and small units (<1.9 km). A generalized linear model with species, spatial grouping, and spatial extent (nested within spatial units) confirmed that this grouping captured most of the spatial-dependent variance in $1/\alpha$ (Table 3, model 2).

Table 2. Summary of the literature survey on dispersal and mobility in European butterflies

	Method or variable measured	Parameter name in the meta-analysis	Number of papers*	Number of species for which data are available	Range of values observed
Multisite mark-release-recapture (MRR)	Negative exponential kernel	$1/\alpha$	28	32	Sites < 1.9 km: $\alpha = 2.55-24.25$ (126.6) Sites > 1.9 km: $\alpha = 0.76-12.19$ (46.14)
	Inverse power kernel	$P5km$	22	30	$P5km = 4 * 10^{-7} - 0.44$
	Mean daily displacement	MDD	19	20	Sites < 0.7 km: $MDD = 23-165$ m Sites > 0.7 km: $MDD = 48-660$ m
	Dispersal fraction	$DISP$	27	25	$DISP = 0-73\%$
	Dispersal mortality	$1/\lambda$	9	8	$\lambda = 0-4.5$
Experiments	Flight speed	$Forest$	1	13	$Forest = 0.5-360$ m.h ⁻¹
	Cage traversal	$Cage$	4	8	$Cage = 0.04-0.43$ h ⁻¹
	Cage exploration	—	2	2	
	Point release	—	2	1	
	Release from height	—	1	1	
	Corridor use	—	1	4	
	Pursue experiment	—	1	1	
	Colonization rate	—	1	1	
	Homing experiment	—	1	1	
Genetic structure	Allozymes	$1 - F_{STA}$	30	27	Continental scale: $F_{ST} = 0.01-0.37$ Regional scale: $F_{ST} = 0-0.27$ Landscape scale: $F_{ST} = 0-0.12$
	Microsatellites	$1 - F_{ST\mu}$	8	7	$F_{ST} = 0.01-0.21$
	RAPD	—	2	2	
	SNP	—	1	1	
	AFLP	—	1	1	
	DALP	—	1	2	
Expert advice	Mobility (<i>sensu lato</i>)	$Expert$	3	142	$Expert = 1-9$
Atlas surveys	Migration	$Migration$	1	19	$Migration = -0.89-0.01$
Transect counts	Vagrancy	$Vagrancy$	1	19	$Vagrancy = 3.16-6$
Behaviour	Time before landing	—	1	4	
	Time in flight	—	1	5	
	Harmonic radar tracking	—	2	3	
Physiology	Flight metabolism	—	1	1	
Occupancy	Mainland (patches)	—	3	3	
	Islands	—	1	1	
	Transect counts	—	3	3	

*Number of papers from which original data are exploitable.

F_{STA} and $F_{ST\mu}$: F_{ST} (a measure of genetic differentiation among local populations) respectively from allozymes and microsatellites.

$P5km$ and $1/\alpha$: descriptors of dispersal kernels (fitted respectively to an inverse power function and to an exponential negative function).

λ : an estimate of the dispersal mortality from the Virtual Migration model.

RAPD: random amplification of polymorphic DNA.

SNP: single-nucleotide polymorphism.

AFLP: amplified fragment-length polymorphism.

DALP: direct amplification of length polymorphisms.

Grouping data in this way would parsimoniously capture the spatial effect. Subsequent analyses of $1/\alpha$ accounted for this scale effect (denoted $Kscale$ for kernel scaling). The long-distance dispersal probability ($P5km$) was insensitive to the spatial extent of the MRR study (Table 3, model 3).

Secondly, we extracted for 20 species their mean daily displacement (MDD), i.e. the mean length of moves between successive captures. MRR experiments were generally planned

in such a way that capture sessions only occurred “weather permitting”, i.e. during periods of butterfly flying activity. Mean distances moved between recaptures could therefore be compared among various field situations. The mean daily displacement was sensitive to the spatial extent of the MRR study (Table 3, model 4). We therefore grouped the data into two spatial scales: large-scale studies where MRR study site was more than the maximal MDD recorded in our data set

Table 3. Generalized linear models with dispersal and mobility of butterfly species as the dependent variable and potentially confounding parameters as independent variables

Generalized linear model	Variable	d.f.	<i>F</i>	<i>P</i>	
1	$1/\alpha = \text{species} + \text{spatial extent}$	32–30	4.68	<0.01	
		Species	31	4.53	0.04
2	$1/\alpha = \text{species} + K_{scale} + \text{spatial extent}(K_{scale})$	Spatial extent	1	4.88	<0.01
		34–28	5.04	<0.01	
		Species	31	4.11	<0.01
		K_{scale}	1	5.01	0.03
3	$P5km = \text{species} + \text{spatial extent}$	spatial extent (K_{scale})	2	1.79	0.18
		30–16	2.26	0.04	
		Species	29	2.33	0.04
4	$MDD = \text{species} + \text{spatial extent}$	spatial extent	1	0.25	0.63
		19–18	2.51	0.03	
5	$MDD = \text{species} + DD_{scale} + \text{spatial extent}(DD_{scale})$	Species	18	1.66	0.14
		spatial extent	1	6.45	0.02
		21–16	5.08	<0.01	
		Species	18	2.92	0.02
6	$DISP = \text{species} + \text{connectivity}$	DD_{scale}	1	11.20	< 0.01
		spatial extent (DD_{scale})	2	0.93	0.41
		24–14	1.66	0.16	
7	$1/\lambda = \text{species} + \text{spatial extent}$	Species	23	0.16	0.17
		Connectivity	1	2.20	0.16
8	$1/\lambda = \text{species} + \text{connectivity}$	7–8	0.67	0.69	
		Species	6	0.77	0.61
9	$1 - F_{STA} = \text{species} + \text{spatial extent}$	spatial extent	1	0.60	0.46
		7–8	0.57	0.77	
10	$1 - F_{STA} = \text{species} + G_{scale} + \text{spatial extent}(G_{scale})$	Species	6	0.63	0.71
		Connectivity	1	0.10	0.76
		27–48	5.95	<0.01	
11	$1 - F_{STA} = \text{species} + G_{scale} + \text{number of populations}$	Species	26	5.88	<0.01
		spatial extent	1	14.14	<0.01
		31–44	6.53	<0.01	
		Species	26	5.68	<0.01
12	$1 - F_{STA} = \text{species} + G_{scale} + \text{number of loci}$	G_{scale}	2	4.48	0.02
		spatial extent (G_{scale})	3	2.52	0.07
		29–46	6.01	<0.01	
		Species	26	5.45	<0.01
13	$1 - F_{ST\mu} = \text{species} + \text{spatial extent}$	G_{scale}	2	6.47	<0.01
		Number of populations	1	0.09	0.77
		29–46	5.99	<0.01	
14	$1 - F_{ST\mu} = \text{species} + \text{number of populations}$	Species	26	5.64	<0.01
		G_{scale}	2	7.45	<0.01
		Number of loci	1	0.01	0.92
15	$1 - F_{ST\mu} = \text{species} + \text{spatial extent}$	7–2	75.82	0.01	
		Species	6	66.45	0.01
16	$1 - F_{ST\mu} = \text{species} + \text{number of populations}$	spatial extent	1	38.55	0.02
		7–2	73.04	0.01	
		Species	6	54.34	0.02
		Number of populations	1	37.07	0.03

$1/\alpha$ and $P5km$: descriptors of the dispersal kernels, fitted to a negative exponential ($1/\alpha$) or to an inverse power function ($P5km$); MDD : mean daily displacement; $DISP$: fraction of dispersing butterflies recorded; λ : patch connectivity at which half of the dispersers die during transfer [inferred from the Virtual Migration model from Hanski *et al.* (2000)]; $1 - F_{STA}$ and $1 - F_{ST\mu}$: indirect (genetic) estimates of dispersal ability, from allozymes and microsatellite studies, respectively; spatial extent: the longest dimension of the study site (in km); G_{scale} , K_{scale} and DD_{scale} : categorical variables for the length of study sites, respectively in allozyme studies, in MRR studies from which dispersal-kernels were drawn and in MRR studies from which we extracted mean daily displacements (see text for details); Connectivity: the mean distance (edge to edge) to the nearest patch in MRR studies.

(>700 m), and small-scale studies where the size of the study site was less than 700 m, which parsimoniously captured the spatial effect on MDD (Table 3, model 5). Subsequent analyses incorporate the scale effect (denoted DD_{scale}).

Thirdly, we used the dispersal fraction, i.e. the proportion of recaptured butterflies that were recaptured in a patch different from that of their first capture in multisite MRR. The dispersal fraction ($DISP$) is available for 25 species. We

suspected that the structural connectivity (i.e. the Euclidian distance between patches) could possibly affect the amount of inter-patch movements, and hence the dispersal fraction. However, we did not detect any significant effect of structural connectivity—here the mean distance (edge to edge) to the nearest patch—on *DISP* (Table 3, model 6).

Fourthly, we used lambda (λ), a parameter estimated by the Virtual Migration model (Hanski *et al.*, 2000) from MRR for eight species. This parameter is the patch connectivity at which half of the dispersers will die during dispersal (for details see Hanski *et al.*, 2000). It therefore combines both the efficiency of butterfly dispersal and the hospitability of the matrix, and decreases with increasing dispersal efficiency. We used $1/\lambda$ to reflect the relative dispersal ability of butterflies. This parameter was not dependent on the size of the study site or on the mean distance to the nearest patch in MRR (Table 3, models 7, 8).

Unfortunately, although a considerable literature exists on patch occupancy dynamics in butterflies (e.g. reviewed in Hanski, 1999), we were unable to use this information in inter-specific comparisons because (1) it was restricted almost entirely to a single species (*Melitaea cinxia*, see Baguette, 2004), and (2) all analyses used standardized data.

(2) Dispersal data from experiments

In a series of experiments, individuals of eight butterfly species were tested in large outdoor cages built in the field station of the Stockholm University in Sweden. These 32 m long cages were typically divided into three sections, with the central region being unsuitable for the butterfly species, i.e. forested for non-forest species, and open for forest species, and the two other sections mimicking the butterfly's habitat (see Norberg *et al.*, 2002 for details on experimental conditions and butterfly manipulations). Cage traversal rate (*Cage*) was recorded in standardized conditions and could therefore potentially serve as a direct estimator of the relative dispersal ability of those eight butterfly species.

In another experiment, Shreeve (1981) reported the speed of marked butterflies crossing non habitat woodlands. From this study, we used the mean speed to cross a small coppiced wood in south Suffolk, available for 13 species and denoted *Forest*. As all butterflies were caught the same year in a common landscape, we did not control for potentially confounding effects of weather or landscape configuration.

(3) Indirect dispersal data

We summarized data on genetic structure inferred from patterns of genetic variation at multiple polymorphic allozyme loci ($N = 27$ species) or microsatellite loci ($N = 7$ species). The F_{ST} , a parameter that reflects the genetic isolation among populations is the most commonly used measure in population genetics. F_{ST} increases with decreasing gene flow among populations. To make the comparison with other dispersal measures easier, we used $1 - F_{ST}$ as an indication of the relative mobility of species.

Two variables were considered: $1 - F_{STA}$ (from allozymes), and $1 - F_{ST\mu}$ (from microsatellites).

In our dataset, $1 - F_{STA}$ was highly sensitive to the spatial extent of the genetic sampling (Table 3, model 9). We therefore grouped allozyme studies according to three spatial scales: the landscape (when the longest dimension of the study was less than 100 km), the region (100–600 km), or the continent (>600 km). This spatial grouping captured most of the spatial-dependent variance in $1 - F_{STA}$ (Table 3, model 10). The number of sampled populations and the number of polymorphic loci scored did not affect $1 - F_{STA}$ in our dataset (Table 3, models 11, 12). So, further analyses accounted for the scale effect only (denoted *Gscale*, for genetic sampling scale).

We detected an effect of the spatial extent of the study site and of the number of populations sampled on $1 - F_{ST\mu}$ (Table 3, models 13, 14). A possible effect of the number of loci scored was not tested due to the lack of available data. Unfortunately, we were unable to control for these confounding effects in subsequent analyses due to the low number of data available for $1 - F_{ST\mu}$ (only seven species).

(4) Mobility

Besides direct and indirect measurement of dispersal, we also found various measures of butterfly mobility (*sensu lato*). Because measuring mobility needs considerable field, laboratory or experimental work, data are extremely scattered. To date, comparative studies have used the presumed mobility of species based on field expert opinion (Cowley *et al.*, 2001; Henle *et al.*, 2004; Komonen *et al.*, 2004; Paivinen *et al.*, 2005; Poyry *et al.*, 2009). Such data are available for most European species.

We considered three sources for expert advice: (1) Bink (1992) assigned a mobility category to most European species (from 1—very sedentary to 9—highly mobile); (2) the ranking of mobility among 49 species according to Cowley *et al.* (2001) who summarized the opinions of 24 experienced European butterfly field experts; and (3) the mobility index of Komonen *et al.* (2004), based on the opinion of 13 butterfly field experts from Finland, who classified 95 butterfly species according to their supposed mobility. Here, we used the rank of each species in our analyses.

These three measures were highly correlated (Pearson's Rhos: Bink *versus* European experts = 0.867, $P < 0.01$, $N = 48$; Bink *versus* Finnish experts = 0.696, $P < 0.01$, $N = 72$ and European experts *versus* Finnish experts = 0.723, $P < 0.01$, $N = 31$). We therefore used only the mobility score of Bink (1992) for further analyses as an indicator of the relative mobility of butterfly species, simply because this variable (*Expert*) was available for a larger number of species (142 species).

Secondly, we used the index for butterfly vagrancy (*Vagrancy*), proposed by Cook, Dennis & Hardy (2001). This index is based on two butterfly surveys in the United Kingdom, from which the authors extracted the relative occurrence of vagrants, i.e. butterfly individuals found in mapping units lacking suitable larval host plants (see Cook

et al., 2001 for details). We averaged those two indices that were highly correlated to obtain a single index of butterfly vagrancy. Vagrancy was calculated for 19 species.

(5) Migration

Another indication of the relative mobility of butterflies is their migration tendency. Several butterfly species are considered migratory, showing seasonally reversed long-distance movements, while others have more subtle tendencies to spread out of their habitats. We used the index of migration ability compiled by Cook *et al.* (2001) and available for 19 species. This index (*Migration*) is based on various criteria, including records outside habitat patches, records in suburban gardens, at-sea sightings and overseas migrations (see Cook *et al.*, 2001 for details). Migration is thus here a measure of the relative tendency of species to show such directed and seasonally reversed mass movements.

IV. DO WE HAVE A CONGRUENT PICTURE OF MOBILITY AND DISPERSAL ACROSS SPECIES?

To compare dispersal and mobility estimates of butterfly species, we used generalized linear models (SAS[®], proc GLM). Whenever necessary, parameters were transformed prior to analysis to fit a normal distribution. We constructed models where two estimates of dispersal or mobility were conflicted: the dependent variable was the dispersal estimate assessed at a larger spatial scale (for instance genetic variables *versus* MRR-derived variables) and the independent variable was the other dispersal or mobility estimate. However, in two cases, this general rule was transgressed to favour a statistical model with a higher number of observations (these two exceptions are identified in Table 4: they appear in the upper-right part of that table).

Some variables used in these analyses were inverted relative to the original data (F_{ST} , α and λ) so that we expect in all cases a positive effect of the independent variable on the dependent variable. Moreover, we standardized each variable to compare their effects among different generalized linear models (GLMs).

Whenever necessary, we incorporated the appropriate scale (that of the dependent variable) as a covariate in the GLM, and grouped the analyses according to the scale of the independent parameter. All GLMs were weighted to correct for the multiple representation of a given butterfly species. When several values were available both for the dependent and the independent variable, the GLMs were constructed with all possible combinations of values, and weighted accordingly.

We noticed a surprising negative relationship between $1/\alpha$ and $1-F_{STA}$ that was due to the contribution of two species with particularly large values for α , the parameter scaling the exponential negative distribution of dispersal distances. Large values of α correspond to a low probability of moving long distances: this parameter ranged from 0.7 to

24.3 in 30 out of 32 species, α was 46.2 for *Pararge aegeria* and 126.6 for *Plebejus argus*. Males speckled wood butterflies (*P. aegeria*) are known to adopt one of two alternative mate-searching strategies: they can either defend a territory and adopt a sit-and-wait strategy, intercepting females passing through their territory, or instead may actively search for mates. Because of their behaviour, the sit-and-wait males have a very high probability of capture, and hence are usually over-represented in MRR datasets. This probable bias was not controlled for and may explain the large value of α measured in *P. aegeria*. An extremely low movement tendency of *Plebejus argus* in UK compared with continental studies has been reported by Thomas & Hanski (1997). Particularities of British landscapes (an island situation associated with extreme human pressures) might explain this difference, which obviously deserves further, quantitative investigations. The kernels of *P. aegeria* and *P. argus* were therefore removed before subsequent statistical analyses. The relationship between $1/\alpha$ and $1 - F_{STA}$ reversed to a positive but non significant trend when we discarded these two outliers.

The various butterfly mobility and dispersal estimates are summarized in Table 4 with details of the statistics shown in Appendix B. Expert advice was highly correlated to several mobility and dispersal measures, among which the migration index of species had the strongest effect. Expert ranking was not significantly related to some other dispersal measures, noticeably the dispersal kernels ($1/\alpha$) measured in small study sites, the mean daily displacement (*MDD*) and the proportion of dispersing butterflies (*DISP*), all measured in MRR studies.

Allozyme-based dispersal estimates ($1 - F_{STA}$) were related to the mean daily displacement measured in large study sites (*MDD*), to butterfly vagrancy and migration and to a lesser extent to expert advice. $1 - F_{STA}$ was also related to the frequency of long-distance dispersal as inferred from MRR studies (*P5km*). $1 - F_{STA}$ was unrelated to the shape of negative exponential dispersal kernels ($1/\alpha$), and was significantly, but negatively, related to the fraction of dispersing butterflies (*DISP*).

Both the negative exponential ($1/\alpha$) and the inverse power (*P5km*) dispersal kernels were best predicted by butterfly vagrancy. The shape of negative exponential kernels was also related to relative flight speed in woodlands (*Forest*) and to the proportion of inter-patch recaptures in MRR (*DISP*), whereas inverse power functions kernels were related to mean daily displacement (*MDD*), to $1 - F_{STA}$ and to migration propensity. Both kernels were not related to butterfly performances in cages.

Butterfly flight speed in forests (*Forest*) was related to the shape of negative exponential kernels ($1/\alpha$), but did not correlate significantly with other dispersal and mobility measures for which the comparison was possible (*Expert*, $1 - F_{STA}$, *P5km*, *Migration*, and *Vagrancy*).

Unfortunately, only a few studies were available for $1 - F_{STU}$, dispersal mortality ($1/\lambda$), and cage traversal making impossible in most cases the comparison with other dispersal measures.

Table 4. Summary of generalized linear models for mobility and dispersal of European butterflies: estimates for the linear effect of the independent dispersal variable. Only significant effects are given (* $P < 0.05$, ** $P < 0.01$, ns: $P > 0.05$). See Appendix B for details of statistics. Numbers in parenthesis are the number of species (N) from which data are available. All variables were standardised which makes direct comparison of linear effects possible. Models were weighted to correct for multiple representation of some species. The dependent variable was the dispersal measure assessed at a larger spatial scale and the independent was the other, except for $1/\alpha$ —*Migration* and *MDD*—*P5km* comparison, for which we transgressed this rule to favour a model with a higher number of observations (results of those GLMs appear in the upper-right part of the table)

Covariate	Dependent variable										
	<i>Expert</i>	$1 - F_{STA}$ <i>Gscale</i>	$1 - F_{ST\mu}$	<i>Migration</i>	<i>P5km</i>	$1/\alpha$ <i>Kscale</i>	$1/\lambda$	<i>MDD</i> <i>DDscale</i>	<i>DISP</i>	<i>Vagranacy</i>	<i>Forest</i>
Independent variable											
$1 - F_{STA}$	—	—	—	—	—	—	—	—	—	—	—
	by <i>Gscale</i>										
	C: 0.572** (9)										
	R: 0.764** (15)										
	L: 0.594** (13)										
$1 - F_{ST\mu}$	ns (7)	NA (<5)	—	—	—	ns (6)	—	0.441** (16)	—	—	—
<i>Migration</i>	0.962** (19)	0.546** (6)	NA (<5)	—	—	—	—	—	—	—	—
<i>P5km</i>	0.387** (27)	0.277* (12)	ns (5)	0.515* (6)	—	—	—	—	—	—	—
$1/\alpha$	by <i>Kscale</i>	by <i>Kscale</i>	NA (<5)	NA (<5)	by <i>Kscale</i>	—	—	—	—	—	—
	A: ns (15)	A: ns (6)	NA (<5)	NA (<5)	A: 0.943** (16)	—	—	—	—	—	—
	B: 0.799** (15)	B: ns (11)	NA (<5)	NA (<5)	B: 0.669** (15)	—	—	—	—	—	—
	0.389* (8)	$N < 5$	NA (<5)	NA (<5)	$N < 5$	ns (5)	—	—	—	—	—
$1/\lambda$	by <i>DDscale</i>	by <i>DDscale</i>	NA (<5)	NA (<5)	by <i>DDscale</i>	by <i>DDscale</i>	—	—	—	—	—
<i>MDD</i>	A: ns (7)	A: $N < 5$	NA (<5)	NA (<5)	A: ns (6)	A: ns (6)	by <i>DDscale</i>	—	—	—	—
	B: ns (15)	B: 1.125** (5)	NA (<5)	NA (<5)	B: ns (12)	B: ns (6)	by <i>DDscale</i>	—	—	—	—
	ns (25)	—0.231** (12)	NA (<5)	NA (<5)	ns (20)	0.243** (20)	ns (8)	ns (15)	—	—	—
<i>DISP</i>	0.764** (19)	0.713* (6)	NA (<5)	0.692** (18)	1.283** (6)	2.032** (6)	NA (<5)	NA (<5)	NA (<5)	—	—
<i>Vagranacy</i>	ns (13)	ns (8)	NA (<5)	ns (11)	ns (6)	0.752* (6)	NA (<5)	NA (<5)	NA (<5)	ns (11)	—
<i>Forest</i>	ns (8)	NA (<5)	NA (<5)	NA (<5)	ns (7)	ns (6)	NA (<5)	NA (<5)	NA (<5)	NA (<5)	NA (<5)

Expert: expert scoring for mobility; F_{STA} and $F_{ST\mu}$: Measure of genetic differentiation among populations (F_{ST}) respectively from allozymes and microsatellites; *Migration*: index of migration ability of butterfly species; *P5km* and $1/\alpha$: descriptors of dispersal kernels; λ : an estimate of the dispersal mortality from the Virtual Migration model; *MDD*: mean daily displacement; *DISP*: proportion of dispersing butterflies in mark-recapture studies; *Vagranacy*: reflects the frequency of outside-habitat records of butterfly species; *Forest*: speed when crossing a small forest in a mark-release-recapture study; *Cage*: traversal rate in outdoor cage experiments; *Gscale*: the scale of the genetic sampling; C = continental scale (>600 km), R = region (100–600 km), and L = landscape (<100 km); *Kscale*: the length of the study site in mark-release-recapture studies used to draw dispersal kernels: A: <1.9 km, B: >1.9 km; *DDscale*: the length of the study site from which mean daily distance was assessed (A: <0.7 km, B: >0.7 km).

V. IS DISPERSAL SPECIES-SPECIFIC?

There was an inherent bias in this review in that some butterfly species were over-represented because their life-histories or their vulnerability to extinction made them favourite model species for research. In particular, there were several studies providing dispersal measures for *Aphantopus hyperantus*, *Boloria aquilonaris*, *Euphydryas aurinia*, *Lycaena helle*, *Lysandra coridon*, *Maniola jurtina*, *Parnassius apollo*, *Parnassius mnemosyne* and *Proclissiana eunomia*. We used the information available from these species to assess the intra-specific variability of dispersal, and to compare this with inter-specific variation in dispersal ability. Of course, our meta-data do not allow a robust comparison between inter- and intra-specific dispersal, mainly because the inter-specific variability can only be measured using the available data, which differ among dispersal estimates, and which are not available for all species. For instance, we found six values for allozyme-based F_{ST} for *Parnassius apollo*, whereas only one dispersal kernel was available for that species. Moreover, phylogenetic relationships among species may constrain the pattern of inter-specific variation in dispersal ability.

We compared the within-species variability in dispersal ability observed in nine species (for which at least four values of at least one parameter are available) to a theoretic distribution of the inter-specific variability. Two parameters of the variability in dispersal ability were considered: the variance and the range of values observed. The comparison was possible for $P5km$, $1/\lambda$, MDD , $DISP$, $1 - F_{STA}$, and

$1/\alpha$, for which multiple data sets were available for at least one species. To build the theoretical distribution of the inter-specific variability for each dispersal estimate, we randomly generated 1000 small-sized samples of our data. To avoid over-representation of the nine model species in these random samples, we only retained one (randomly chosen) value for each model species before the bootstrap procedure. We next compared the within-species variability in dispersal ability (for each of the nine model species) to the inter-specific variability observed in the 1000 samples of similar size. If dispersal ability is species-specific, the intra-species variability would be lower than the inter-species variability, and the observed variability (either the variance or the range in the dispersal estimate) would be less than the 95% confidence interval of the theoretical distribution (left-tailed P-value). If dispersal ability is not significantly less variable at the intra-specific level than at the inter-specific level, then the observed inter-specific variability would fail into the 95% confidence interval of the theoretical distribution obtained from bootstrap. Observed variability at the intra-specific level greater than the 0.95 percentile of the theoretical distribution (right-tailed P-value) would indicate that the dispersal estimate is more variable at the intra-specific level than at the inter-specific level.

Table 5 shows that within-species variability was less than the inter-specific variability in $1 - F_{STA}$ for three species (left-tailed P-value <0.05). Intra-species variability in other dispersal estimates was not significantly lower than inter-specific variability (P > 0.05), and was even significantly larger for MDD in *Parnassius apollo*.

Table 5. Comparison of intra-specific variability in dispersal estimates to the inter-specific variability in random samples of the same size. N = sample size. *left-tailed P-value <0.05, **left-tailed P-value <0.01

Dispersal parameter	Model species	N	Variance	P (variance)	Range	P (range)
$1/\alpha$	<i>Boloria aquilonaris</i>	7	10.06	0.215	8.12	0.164
	<i>Euphydryas aurinia</i>	5	9.73	0.270	8.07	0.303
	<i>Maniola jurtina</i>	6	20.83	0.627	12.27	0.649
	<i>Proclissiana eunomia</i>	8	9.14	0.150	8.10	0.108
$P5km$	<i>Boloria aquilonaris</i>	6	0.00014	0.149	0.026	0.114
	<i>Maniola jurtina</i>	5	0.00020	0.270	0.033	0.269
MDD	<i>Euphydryas aurinia</i>	7	27765	0.836	491	0.935
	<i>Lycaena helle</i>	5	1439	0.106	92	0.117
	<i>Maniola jurtina</i>	4	14921	0.668	272	0.666
	<i>Parnassius apollo</i>	5	57424	0.997	503	0.979
$DISP$	<i>Aphantopus hyperantus</i>	4	0.030	0.409	0.423	0.493
	<i>Euphydryas aurinia</i>	5	0.026	0.309	0.409	0.335
	<i>Maniola jurtina</i>	4	0.059	0.703	0.538	0.708
	<i>Proclissiana eunomia</i>	6	0.039	0.507	0.473	0.384
$1 - F_{STA}$	<i>Euphydryas aurinia</i>	7	0.00259	0.535	0.154	0.586
	<i>Lysandra coridon</i>	6	0.00039	0.081	0.054	0.100
	<i>Maniola jurtina</i>	7	0.00021	0.012*	0.034	0.004**
	<i>Parnassius apollo</i>	6	0.00677	0.759	0.022	0.003**
	<i>Parnassius mnemosyne</i>	8	0.00059	0.130	0.066	0.106
	<i>Proclissiana eunomia</i>	6	0.00027	0.040*	0.043	0.049*

$P5km$ and $1/\alpha$: descriptors of dispersal kernels; MDD : mean daily displacement; $DISP$: proportion of dispersing butterflies in mark-recapture studies; F_{STA} and $F_{ST\mu}$: F_{ST} respectively from allozymes and microsatellites.

VI. DISCUSSION

Dispersal in butterflies is a very active research field. The great efforts made to describe dispersal and mobility in butterflies using various direct and indirect methods have inevitably resulted in a high heterogeneity within the available data (Table 2). However coherent patterns emerged from these data (Table 4). The meta-analysis of a data set based on information from 81 papers found that dispersal estimation was highly variable, both between and within species (Tables 4,5). Thomas (1984) was the first to highlight inter-specific variability in dispersal, by contrasting species with “closed” populations with species with “open” populations, a classification that is now rather obsolete (J. Thomas, personal communication). Our knowledge of the dispersal process has increased considerably over the past decades in parallel with the understanding of the key role of dispersal in the dynamics and evolution of spatially structured populations. While Thomas’ (1984) paper attempted to show that the spatial scales of butterfly population dynamic studies were much more restricted than those then used in the study of other model insects, his pioneering insight that different butterfly species used landscapes in different ways paved the way for the emergence of metapopulation theory, in which butterflies played a central role (Thomas, Thomas & Warren, 1992; Hanski & Kuussaari, 1995).

Intra-specific variability in dispersal has been investigated by comparison of direct dispersal estimates for the same species in contrasting landscapes (e.g. Baguette, 2003; Schtickzelle *et al.*, 2006), as well as by recent studies exploiting landscape genetics (e.g. Keyghobadi, Roland & Strobeck, 2005). These empirical studies so far support the statement that the existence of a species-specific dispersal function is probably a myth (Clobert, Ims & Rousset, 2004).

Below, we address these two levels (inter- and intra-specific) of variability in dispersal in butterflies. We will consider the various biases that exist in our dataset, and we will try to evaluate how they might affect the general picture of dispersal arising from this review. Our final aim is to identify future research questions to provide advances in the field of dispersal.

(1) Inter-specific variability in dispersal

Overall, we found weak evidence for associations between F_{ST} estimates and the shape of dispersal kernels. The most commonly used dispersal index, the negative exponential dispersal kernel ($1/\alpha$), was unable to predict differences in gene flows across butterflies, while inverse power kernels had a only a slight (but significant) relationship with $1 - F_{STA}$ (Table 4). This discrepancy might have several sources. Firstly, genetic-based dispersal estimates sum two processes: the amount of dispersal movements and the relative contribution of dispersers to the next generation (effective dispersal). However, only a small fraction of male butterflies generally participate in reproduction (e.g. Suzuki & Matsumoto, 1992). To the best of our knowledge, only

two studies attempt to relate effective dispersal to the amount of dispersal movements in butterflies (Vandewoestijne & Baguette, 2004a; Vandewoestijne *et al.*, 2008), and we therefore cannot investigate whether this relationship differs among species. It is a difficult issue that certainly deserves further attention. Such efforts have been made for other taxonomic groups (lizards: Sinervo *et al.*, 2006; birds: Gonzalez *et al.*, 2006; plants: Gonzalez-Martinez *et al.*, 2006; damselflies: Watts *et al.*, 2007). Provided that non-invasive genetic markers are developed (see below), we are convinced that butterflies would be excellent model species to address this critical issue. The coupling of multi-site MRR studies with landscape genetics would also benefit from additional behavioural investigations measuring the effective size of populations. Combination of these three kinds of data would allow direct comparisons of genetic and ecological estimates of dispersal.

Secondly, dispersal kernels and F_{ST} were not inferred at the same spatial scale: the median study size was 1.9 km in MRR and 100 km in allozyme studies. A recent empirical study (Bonte, De Clercq & Zwertvaegher, 2009) showed that short- and long-distance dispersal processes could result from different selective pressures. These two processes might thus theoretically have followed uncoupled evolutionary histories among butterflies (see Van Dyck & Baguette, 2005), but this has still to be investigated.

Finally, the lack of convergence between dispersal kernels and F_{ST} estimates could be due to the fact that MRR studies were mainly performed in altered (fragmented) landscapes. In such fragmented landscapes, dispersal is expected to be more costly than in landscapes with better connectivity (Olivieri & Gouyon, 1997; Heino & Hanski, 2001; Schtickzelle *et al.*, 2006). As allozyme-derived F_{ST} mostly reflects past gene flows, dispersal ability observed in fragmented landscapes might no longer correspond to dispersal in ancestral generations, at least for some butterfly species (Vandewoestijne & Baguette, 2004b). Unfortunately, suitable studies to test this hypothesis are lacking.

Genetic-based dispersal estimates offer a powerful, although indirect, estimate of dispersal ability of species. Because they sum dispersal events over a large number of generations and over large spatial scales, F_{ST} estimates alleviate spatial and temporal variability in dispersal expression. This was highlighted by our analysis of within-species variability in dispersal estimates: only F_{ST} estimates were significantly less variable within species than at the inter-specific level (Table 5). Moreover, because they are based on gene flow, and hence on effective dispersal (dispersal followed by successful reproduction of dispersers), genetic-based dispersal estimates directly reflect the part of dispersal that is relevant to evolutionary issues and to demographic changes in populations and metapopulations (see e.g. Vandewoestijne *et al.*, 2008). Notice however that even non-effective dispersal events might indirectly induce demographic changes in populations, for example through density-dependence. Genetic population structuring moreover allows the detection of slight differences in dispersal

ability between species, even in cases of very low dispersal rates that are inherently difficult to detect by direct methods, or by contrast for species with very high dispersal abilities, which would require very large study sites for MRR work.

Nevertheless, F_{ST} and other estimates of genetic structuring are not the final solution to dispersal estimates. As mentioned above, they alleviate the effects of recent or local changes in dispersal patterns, which might be of prime importance when considering the response of species to environmental alterations such as fragmentation or climate change. Moreover, genetic structuring among populations can be insufficient to allow detection of dispersal patterns at very small spatial scales. However, genetic data can be used not only to infer the genetic differentiation among populations, but also to provide information on recent dispersal flows through assignment tests. Assignment tests allow the successful detection of immigrants and their progeny even in cases of moderate dispersal rates among populations (<30% each generation: Wilson & Rannala, 2003; Latch *et al.*, 2006). As they require much less fieldwork than traditional MRR studies, such assignment tests might therefore be a valuable surrogate for MRR studies (Berry, Tocher & Sarre, 2004).

Allozyme-derived F_{ST} values are now available for many species (Table 2) and could theoretically be obtained for many more butterflies at relatively low cost. However, the generalization of their application could be detrimental for species persistence. Allozyme purification requires the sacrifice of individuals. The allozymic data used in this meta-analysis required killing more than 22000 adult butterflies in total (from 27 species), which seems ethically questionable in times where non-invasive genetic markers are increasingly available. Although microsatellite development is difficult in butterflies (see, for instance, Neve & Meglecz, 2000), these non-invasive markers are now available for at least seven European species (Harper *et al.*, 2000; Habel *et al.*, 2005; Petenian *et al.*, 2005; Sarhan, 2006; Zeisset *et al.*, 2008) and future technical progress will hopefully allow development of primers for other species. Despite the fact that the small sample size precluded comparison between the results obtained from allozymes and from microsatellites, we firmly encourage the development of the latter, or that of other markers based on polymerase chain reaction (such as Single Nucleotide Polymorphisms) in butterflies.

Despite the high heterogeneity in dispersal and mobility data (Table 2), the small sample size available for some comparisons, and high intra-specific variability (Table 5), we were able to detect a general pattern in the organization of dispersal ability across species (Table 4). In particular, *vagrancy* was able to capture differences in dispersal ability among species. This index, developed by Cook *et al.* (2001), is calculated from the proportion of butterfly sightings occurring in 1 ha plots lacking suitable caterpillar host plants, recorded in standardized and repeated transect counts (>25 passages in 30 plots). *Vagrancy* is strongly related to both the shape of dispersal kernels measured at the kilometre scale

($P5km$ and $1/\alpha$), and to gene flows measured at larger spatial scales ($1 - F_{STA}$: from tens to hundreds of kilometres).

Some minor restrictions preclude the application of *vagrancy* measures to all butterfly species: *vagrancy* cannot be measured for species with poorly known larval feeding regimes, for those for which field determination of species is impossible, or for those with very common host plant species. Moreover, environmental conditions may affect *vagrancy* behaviour, hindering comparison of *vagrancy* in contrasting environments, and hence, preventing the relative ranking of *vagrancy* for species with non overlapping distributions. Nonetheless, *vagrancy* seems a promising parameter for the rapid assessment of the relative dispersal ability of most butterfly species.

Our meta-analysis showed that the mobility scores of experts reflected the migration tendencies of species more than their dispersal abilities (Table 4). The relatively low predictive power of experts could be due to the fact that, as highlighted in this study, the amount of published information on dispersal varies greatly from species to species (Table 2, Appendix A), while information on migration is available for most species, for instance in identification field guides. Experts can only assess butterfly mobility from known migration status and from field experiments, which can be influenced by confounding traits (wing size, length of flight period, or number of generations, for instance) and by phylogenetic relationships among species. The probable influence of phylogeny and life-history traits on expert ranking on the one hand and on realized dispersal on the other deserves further investigation.

Expert advice offers the undeniable advantage of its being available for most butterflies of Western Europe (Bink, 1992). This geographic coverage could be increased by sending the questionnaire used by Cowley *et al.* (2001) to experienced lepidopterologists from every region of interest. However, this procedure cannot be applied at global scale, due to the lack of field experts in many regions of the world. Due to the low predictive power of expert scoring, we recommend using this parameter only as an indication of the relative dispersal ability of butterflies for comparisons among large numbers of species. Indeed, the effect of mismatches between expert advice and real dispersal abilities would be deleteriously amplified for small sample sizes.

The mean daily displacement (*MDD*) is a measure commonly extracted from multisite MRR experiments. Despite the relatively large number of species for which it is available, we generally did not find a significant relationship between *MDD* and other dispersal and mobility measures. However, we noticed significant positive relationships with $1 - F_{STA}$ (when *MDD* was measured in large study sites) and with $P5km$ (when the size of the study site was set as the dependent variable). The inability of *MDD* to predict interspecific differences in dispersal ability could be due to the fact that this parameter typically may confound routine (foraging) movements and special dispersal movement between suitable patches (see Table 1), particularly when *MDD* is measured in small study sites (see Van Dyck & Baguette, 2005).

The decisions to leave a habitat patch, and then to cross unsuitable areas to find another habitat patch are unlikely to depend only on an individual's flying ability. This is nicely exemplified by a MRR study in which any between-patch movements were recorded for an inter-patch distance of 100 m, whereas within-patch movements of 250 m were recorded (Thomas, 1983). The behavioural decision involved in dispersal is clearly ignored in *MDD*, while it is explicitly accounted for in most other dispersal estimates. This difference might explain the lack of relationships between *MDD* and other measures. Dispersal kernels also do not explicitly distinguish inter-patch movement from routine movements (Table 1). However, as MRR study landscapes are generally highly fragmented, within-patch movements are often grouped together within the first distance class in dispersal kernels (generally 0–50 m or 0–100 m).

The dispersal fraction, *DISP*, i.e. the proportion of recaptures occurring outside the patch of first capture, was not related to most other dispersal estimates (Table 4), with the exception of a weak positive relationship with negative exponential kernels ($1/\alpha$) and a weak negative relationship with $1 - F_{STA}$. This was an indication that *DISP* cannot serve as a surrogate for dispersal ability of butterflies, and particularly for the assessment of long-distance dispersal ability. A technical bias might have caused this pattern. Authors generally did not agree in their definition of habitat patches; this is emphasized by several recent publications that propose the adoption of a resource-based definition of habitat rather than the definition of suitable areas based on vegetation types (e.g. Dennis, Shreeve & Van Dyck, 2003; Turlure *et al.*, 2009). Over- or under-estimation of the number of patches would lead to inaccurate calculation of the relative number of interpatch movements. Another explanation could be that *DISP* did not differentiate between short- and long-distance movements. These two types of movement could undergo separate selection processes (Bonte *et al.*, 2009), and hence could contribute differently to the genetic structuring of populations (and hence to F_{ST}).

Experimental assessments of dispersal and mobility (*Cage* and *Forest*) used in the meta-analysis fail to reflect convincingly differences in dispersal or mobility across species (Table 4). However, the main aim of these experiments was not to assess relative dispersal ability but to address specific questions about the impact of certain habitats (predominantly forests) on landscape connectivity (i.e. the way a landscape allows or impedes dispersal movements: With, Cadaret & Davis, 1999) for various butterfly species. Because they quantified differences in the ability to cross forests (or potentially other habitats of interest), such experiments are helpful to parameterize individual-based dispersal models, least-cost distance (e.g. Stevens *et al.*, 2006) or diffusion models (e.g. Ovaskainen, 2004). In these models, the fate of a disperser crossing the landscape between two habitat patches depends on its ability to cross less suitable elements of the landscape, which in turn depends on its flight speed in those elements (measured by the variable *Forest*) and on the permeability of the boundaries between suitable habitats

and unsuitable habitats (measured in cage experiments), among other factors. The development of such models for butterflies, especially the individual-based models coupling such behavioural data to dispersal estimates, is clearly an exciting perspective.

(2) Intra-specific variability in dispersal

Our meta-analysis showed a difference in the pattern of within-species variability between dispersal indices taken from multisite MRR experiments on the one hand, that are highly variable at the species level, and genetic-based measures on the other, that appear rather fixed for a given species (Table 5). This pattern may have several causes. Firstly, as mentioned above, one of the advantages of the genetic estimation of dispersal is that it reduces the effect of both spatial and the temporal variability in dispersal. By contrast, field quantification of dispersal is affected by factors other than the organism's propensity to disperse. This might explain the high within-species variability in MRR-derived variables and the low within-species variability for F_{ST} estimates. Our analysis controlled for potential biases due to scaling, distance to the nearest neighbour, and the number of populations or loci scored (Table 3), but we were not able to control for other biases in measures of dispersal behaviour such as weather or landscape connectivity effects. However, dispersal flows might be highly variable from year to year, and among landscapes of varied connectivity (see e.g. Schtickzelle *et al.*, 2006), which may have enhanced the within-species variability in MRR-derived dispersal estimates.

Secondly, this pattern of within-species variability may be an artefact of the meta-analysis. The theoretical distribution of dispersal variation we used at the inter-specific level depended on the data available for the bootstrap. Roughly the same number of species, genera and families were represented in genetic and MRR data (Table 2), making underestimation of inter-species variability unlikely. However, some MRR studies specifically focused on dispersal patterns in landscapes of contrasting structural connectivity (see for instance Schtickzelle *et al.*, 2006), which might have artificially enhanced the within-species variability in our MRR-based dispersal indices.

Thirdly, genetic data only accounted for effective dispersal and therefore might be very different from raw movement data. Those differences might be particularly exacerbated in butterflies with a long flight period that have time for movements among several habitat patches, and for which many ineffective movements could be recorded in MRR studies. Only four species were well represented both in the genetic and in the MRR studies (Table 5), making it impossible to test this hypothesis. Nevertheless, among these, the two species with a short flight period (*Euphydryas aurinia* and *Proclossiana eunomia*) had comparable variances in their genetic and MRR-based dispersal estimates (high variances for *E. aurinia*, low variances for *P. eunomia*), while two species with a long flight period (*Maniola jurtina* and *Parnassius apollo*) had consistently large variances in MRR-based dispersal estimates. This hypothesis requires testing by (1) comparing

the adult survival of these four species in relation with their lifetime movement paths, and (2) of course, estimating these parameters using more species.

(3) Technical biases

Meta-analyses inherently have to account for heterogeneity in the available data. In addition, negative results are generally not presented in published material. However, negative results are unlikely to exist regarding dispersal ability itself, making this bias unlikely in our meta-analysis: as we expect that at least some dispersal will occur, when no between-patch movement is observed the result is likely to be reported. Another potential bias could be due to the fact that some studies specifically addressed the variability of dispersal, which may have artificially enhanced the within-species variability in our meta-analysis. However, in many cases, this within-species variability was measured in independent studies.

Another typical bias arises from semantic inconsistencies. However, we carefully checked for all studies in this analysis which parameters were presented, how these were measured and how they were presented therein. Whenever necessary, we corrected these parameters in order to obtain comparable data. For instance, no-movement data (that is the portion of recaptures with dispersal distance = 0) were sometimes omitted from the MRR data presented, so, we used the number of recaptures to correct this bias.

The main source of artefacts in our meta-analysis was the inherent differences between field and technical conditions. We standardized as far as possible the selected data, and controlled particularly for the spatial scale of the study, the configuration of the landscape, the genetic markers, the number of loci scored, or the number of populations sampled (Table 3). We showed that the spatial scale at which dispersal was addressed did influence the performance measured (Table 3), as noted previously by Schneider (2003) for MRR data. Small-scale studies appeared generally less informative than large-scale studies (Table 4). We therefore encourage researchers to choose large study sites over small ones.

We were unable to control for potential biases in allozyme-derived F_{ST} estimates due to the presence of loci under selection. We discarded from our data one F_{ST} value that was derived from a set of loci among which two were proved to be under selection in the sample considered [phosphoglucosmutase (PGM) and isocitrate dehydrogenase (IDH-2): Goulson, 1993]. Other studies not considered here reported the signature of selection for phosphoglucosmutase (PGI), which may be related to the expression of dispersal (Watt, Donohue & Carter, 1996; Haag *et al.*, 2005). We could not control fully for that potential bias because (1) most studies did not control for selective pressures acting on the loci considered, and (2) all studies did not show which particular loci were used to infer F_{ST} estimates, which precluded systematically discarding PGM, IDH-2 or PGI.

Finally, we were unable to control for potential biases in MRR results due to climatic conditions or to population

densities, which may both affect the expression of dispersal. Weather conditions may differ across years and, within a given year, from place to place. Moreover, the effect of a particular climatic condition, for instance a particularly dry or hot spring, may influence dispersal differently in different butterfly species. We cannot test for those biases which would have required repeated MRR surveys across years, sites and species. Dispersal is known to be density-dependent in several butterflies (Baguette *et al.*, 1998; Enfjall & Leimar, 2005), and the direction of this dependence varies according to species and sex. Unfortunately, butterfly densities were often not reported in published material, which hindered the ability to control for density-dependent dispersal.

(4) Perspectives

A general pattern in the organization of dispersal ability has emerged from this meta-analysis of the various methods used to measure dispersal in butterflies. Nonetheless, we did not investigate the evolutionary pathways that might explain that pattern and the differences observed between long-distance dispersal and short-distance dispersal. Because it drives gene flow, and hence modifies the evolutionary conditions in populations, dispersal cannot be considered independently from other life-history traits. Understanding the way dispersal evolved in butterflies therefore needs us to focus both on the phylogenetic relationships among species and on the trade-offs between dispersal and other life-history traits. Ideally, those trade-offs should be addressed both across species and at the intra-specific level.

Our meta-analysis also showed that we need to investigate the relationship between movement rates and effective dispersal rates. Because effective dispersal has a key role in both the dynamics and the evolution of populations, this parameter is of prime importance in the response of populations to habitat fragmentation and climate change (see e.g. butterfly examples in Settele *et al.* 2008; Thomas, Simcox & Clarke, 2009). Advances in landscape genetics, and particularly the development of Bayesian tools for assignment tests (e.g. Wilson & Rannala, 2003; Berry *et al.*, 2004; Latch *et al.*, 2006), and advances in individual-based approaches, will allow crucial insights on that part of dispersal. We therefore strongly encourage the development of non-invasive genetic markers (microsatellites, SNPs) to allow such promising analytical tools to be used in a wide variety of field situations to disentangle the processes underlying effective dispersal.

Finally, our exploration focussed mainly on the patterns of variation of dispersal across and within species. Our literature search revealed that the processes generating such patterns still remain poorly known. The explanations of the observed variations in dispersal are often suppositions without formal tests. Individual-based models offer an excellent opportunity to perform such tests. Accordingly, we suggest that the rich database accumulated on butterflies provides an excellent opportunity for evolutionary ecologists to test hypotheses of the proximate and ultimate factors driving dispersal.

We suggest that future research focuses on (1) the relationships between movement rates and effective dispersal rates in the context of environmental changes, (2) the processes underlying the observed patterns in within-species variation in dispersal ability, (3) how habitat quality and environmental changes affect the expression and the evolution of dispersal in an ever-changing world.

VII. CONCLUSIONS

- (1) In the rich literature on butterfly dispersal and movement abilities there is a high degree of heterogeneity in the methods used. Dispersal ability was assessed either by direct measurements, through multisite mark-release-recapture studies and experiments, or by indirect (genetic) methods. In addition, studies did not use the same definition of dispersal, and other types of butterfly movement were addressed such as seasonal migration and ordinary foraging and vagrancy movements.
- (2) Both direct and indirect estimates of dispersal ability could be biased by the spatial scale over which they were assessed. Investigations carried out at small spatial scales were less informative than those in large study sites. We recommend that larger study sites should be used for the investigation of dispersal.
- (3) Despite the heterogeneity in methods, we found a rather congruent picture of how dispersal and mobility abilities are distributed across butterfly species. Vagrancy measures were the most reliable in assessing the relative ability of species to disperse, whereas expert scoring reflected rather the migration propensity of species than their dispersal ability.
- (4) Dispersal performance was highly variable within each butterfly species. This variation was particularly high for directly assessed performance, whereas it was lower for indirect (genetic) estimates of dispersal.
- (5) The low inter- and intra-specific variability of classical estimates of genetic structure (here F_{ST}) precluded their application for the investigation of context-dependence in dispersal. However, more recent genetic tools guaranteed the efficiency of molecular markers in this investigation.
- (6) Promising avenues for future research are: (a) the relationships between movement rate and effective dispersal rate in the context of environmental changes, (b) the processes underlying the observed pattern in within-species variation in dispersal ability, (c) how habitat quality and environmental changes might affect the expression and the evolution of dispersal.

VIII. ACKNOWLEDGEMENTS

Sofie Vandewoestijne, Benjamin Bergerot and Jan Christian Habel kindly provided precious unpublished dispersal data:

we warmly thank them for this. We thank the members of the Evoltrait team (MNHN, UMRS CNRS-MNHN 7179), of the Quantitative Conservation Biology and Behavioural Ecology groups at Université Catholique de Louvain (UCL) for stimulating discussion, with a special mention to Hans Van Dyck who made valuable comments on our results. We also thank Josef Settele and Justin Travis for their helpful comments. Funding and other resources were generously provided by the European Union FP7 SCALES program.

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