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REVIEW AND SYNTHESIS

A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals

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Abstract

Dispersal, the behaviour ensuring gene flow, tends to covary with a number of morphological, ecological and behavioural traits. While species-specific dispersal behaviours are the product of each species' unique evolutionary history, there may be distinct interspecific patterns of covariation between dispersal and other traits ('dispersal syndromes') due to their shared evolutionary history or shared environments. Using dispersal, phylogeny and trait data for 15 terrestrial and semi-terrestrial animal Orders (> 700 species), we tested for the existence and consistency of dispersal syndromes across species. At this taxonomic scale, dispersal increased linearly with body size in omnivores, but decreased above a critical length in herbivores and carnivores. Species life history and ecology significantly influenced patterns of covariation, with higher phylogenetic signal of dispersal in aerial dispersers compared with ground dwellers and stronger evidence for dispersal syndromes in aerial dispersers and ectotherms, compared with ground dwellers and endotherms. Our results highlight the complex role of dispersal in the evolution of species life-history strategies: good dispersal ability was consistently associated with high fecundity and survival, and in aerial dispersers it was associated with early maturation. We discuss the consequences of these findings for species evolution and range shifts in response to future climate change.

Keywords

Age at maturity, dispersal costs, dispersal phenotypes, fecundity, global change, life-history trade-offs, phylogenetic signal, survival, thermoregulation, trophic levels.

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"MB, JC, JFLG and VMS dedicate their contribution in this work to the memory of the late Robert Barbault, who has been an essential linchpin in the development of modern ecology in France."

INTRODUCTION

Dispersal syndromes describe patterns in the covariation across species, populations or individuals of morphological, behavioural or life-history traits associated with dispersal, a behaviour that sustains gene flow and influences adaptation in natural populations (Ronce 2007; Clobert *et al.* 2012). The existence of distinct dispersal syndromes is a consequence of different proximate and ultimate mechanisms for which a thorough review is given in Ronce & Clobert (2012). At the proximate level, covariation between dispersal and another trait may come from genetic correlations between traits due to linkage disequilibrium or the pleiotropic effects of genes controlling the dispersal phenotype. In addition, dispersal and other traits may also respond in parallel to changes in environmental conditions and selective pressures may lead to co-evolutionary dynamics between dispersal and life history, behaviour or morphology. Finally, dispersal and other traits may reciprocally affect each other's expression or evolution (Fig. 1).

Understanding dispersal syndromes is important for several reasons. First, accurate descriptions of patterns of covariation between dispersal and other traits enable a better understanding of the proximate and ultimate causes of dispersal (Kisdi *et al.* 2012). Second, the existence of dispersal syndromes

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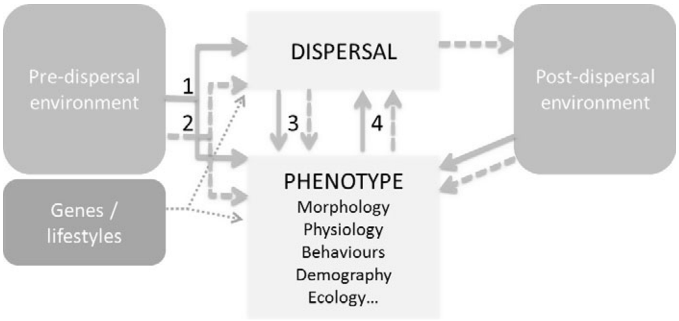

Fig. 1 Hypothetical mechanisms underlying dispersal syndromes. Phenotype: any dimension of the phenotype other than dispersal. Plain lines illustrate selection pressures; dashed lines show environmental (plastic) effects; dotted lines illustrate the genetic covariation among traits and the effect of lifestyles. Numbers refer to text. Modified from Ronce & Clobert 2012.

raises the interesting possibility that dispersal could indirectly affect the social, demographic or genetic processes in populations, as well as interactions between species in communities, via the so-called trait-based effects of dispersal (Benard & McCauley 2008; Clobert *et al.* 2009; Ronce & Clobert 2012). Third, the characterisation of dispersal syndromes across a phylogeny in well-studied species may help in predicting dispersal patterns in closely related, rare or cryptic species (e.g. the prediction of dispersal distances or rates: Sekar 2012; Stevens *et al.* 2013; Whitmee & Orme 2013). Many management strategies implemented in biodiversity conservation require at least basic data on dispersal. For example, the reintroduction of endangered species, the management of invasive species and the implementation of reserve networks all rely on realistic assumptions about dispersal patterns. Finally, the description of dispersal syndromes can provide new perspectives to understand the constraints and trade-offs associated with movement behaviour. This may help identify potential costs associated with dispersal (Bonte *et al.* 2012), which is useful to assess landscape connectivity for conservation purposes (Baguette *et al.* 2013).

Dispersal syndromes have been identified independently in several taxonomic groups, but we still lack a comprehensive view of their patterns and consistency at the large taxonomic scale. For instance, a positive covariation between dispersal and body size was detected in birds (Böhning-Gaese *et al.* 1998; Paradis *et al.* 1998; Sutherland *et al.* 2000; Dawideit *et al.* 2009), mammals (Sutherland *et al.* 2000; Whitmee & Orme 2013) and butterflies (Sekar 2012; Stevens *et al.* 2012), but this relationship seems variable among taxa and even within species, being generally positive, but sometimes negative (Bowler & Benton 2005; Sinervo *et al.* 2006). Similarly, recent lines of evidence indicate that dispersal is also integrated into life histories via complex patterns of trade-offs and co-adaptation among traits (Fjerdingstad *et al.* 2007; Ronce & Clobert 2012; Stevens *et al.* 2012). Dispersal is thus predicted to be an additional axis of life-history strategy for many species (Burton *et al.* 2010), where variation was historically organised along purely demographic axes, such as the slow–fast continuum opposing r and K species on one axis and the age at maturity continuum opposing semelparous (reproducing only once) and iteroparous species (with multiple reproductive events) on the second axis (Gaillard *et al.* 1989, 2005; Clobert *et al.* 1998). Information on the relationship between dispersal and demographic tactics are still largely unknown as, until now, there has been a lack of comparative data across taxa.

Here, for the first time, we undertake a comparative analysis of dispersal syndromes across a wide variety of taxonomic groups. Rather than focusing on one particular dispersal syndrome (e.g. dispersal-body mass allometry), we utilise data from several morphological, life-history and behavioural traits, which are hypothesised to correlate with dispersal behaviour. Using several working hypotheses, we test predictions for each dispersal syndrome (see below) based on evolutionary theory and empirical studies. We also test the existence of a single, universal dispersal syndrome across all taxa. In the event that a universal dispersal syndrome cannot be identified, we examine how species lifestyles could drive variation in dispersal syndromes between taxonomic groups.

Dispersal can evolve rapidly by adaptive processes (e.g. Stevens *et al.* 2010a) enabling a fast adjustment of dispersal to new environmental conditions (e.g. Schtickzelle *et al.* 2006; Perkins *et al.* 2013), but the extent to which dispersal evolution is constrained by common ancestry remains poorly known. We therefore also quantify the distribution of dispersal traits across the phylogeny of taxonomic groups (i.e. phylogenetic signal), which provides an indication on how common ancestry influences dispersal evolution.

Our comparative analysis of several dispersal syndromes is based on the test of a suite of working hypotheses derived from the framework proposed by Ronce & Clobert (2012) to understand the origin of dispersal syndromes (Fig. 1), namely:

(1) Syndromes may emerge from the *joint selection of several traits under a common pressure* (path 1 in Fig. 1). For instance, habitat instability can select for the evolution of higher dispersal rates and distances (Shapiro 1975) as well as for a demographic strategy that enables rapid population growth (Baker & Stebbins 1965; Burton *et al.* 2010). From this mechanism, we hypothesise that high dispersal ability associates with high fecundity, low survival rate and early maturation.

(2) Environmental conditions may also cause dispersal syndromes when *the expression of several traits is affected by the same environmental factor* across species (path 2 in Fig. 1). In particular, life-history theory predicts allocation trade-offs between demanding traits when time and energy are limited (Stearns 1976). We therefore expect to observe a trade-off between dispersal and fecundity (e.g. Johnson 1969), as well as between dispersal and other time- or energy-consuming behaviours (e.g. parental care).

(3) Syndromes may also arise when *dispersal itself constrains the evolution or the expression of other phenotypic traits* (path 3 in Fig. 1). In particular, the evolution of specialisation is influenced by the movement behaviour of organisms, including dispersal rates and distances (Poisot *et al.* 2011). Levins (1962) first proposed that very low dispersal capacity generally favours the evolution of local specialisation, whereas higher dispersal rates or distances result in evolution towards generalism, an idea confirmed by Brown & Pavlovic (1992) and Nurmi & Parvinen (2008). However, other co-evolutionary dynamics

between dispersal and generalism are predicted, where specialists are favoured for intermediate dispersal rates and generalism evolves for low and high dispersal rates (Ronce & Kirkpatrick 2001; Kisdi 2002; Nurmi & Parvinen 2008). A dispersal syndrome where generalists and specialists show differing dispersal characteristics is therefore expected, although the directionality of the relationship is not identified *a priori*.

(4) The mirror situation may also cause dispersal syndromes, when *a phenotypic trait influences selection on dispersal* (path 4 in Fig. 1). Accordingly, any trait increasing dispersal benefits and reducing dispersal costs may ultimately favour the evolution of higher dispersal (Bonte *et al*. 2012). For instance, in spatially homogeneous environments, higher adult survival means more competition among adults, hence selection for more dispersal, but it also means less vacancies for immigrants, hence selection for less dispersal. Overall, this can lead to the evolution of higher dispersal with increased survival or to a bell-shaped relationship between dispersal and survival (Olivieri *et al*. 1995). In spatially heterogeneous environments, generalists experience landscapes at a finer grain than specialists as they use higher proportions of the available habitat compared with specialists. In such fine-grained landscapes, dispersal costs are reduced, which selects for higher dispersal propensity (Baguette & Van Dyck 2007). Dispersal costs may also be reduced in long-lived organisms, as longevity increases opportunities to meet favourable conditions for dispersal. A higher fecundity increases competition among relatives, which selects for more dispersal (Hamilton & May 1977; Clobert *et al*. 2004; Bowler & Benton 2005; Ronce 2007). Longer parent–offspring association may also increase parent–offspring competition for resources, increasing the benefits of dispersal in species with more intense parental care. Dispersal costs might also change with the locomotor mode and nycthemeral activity patterns (Bonte *et al*. 2012). Dispersal costs can, for instance, be reduced by enhanced locomotion efficiency in large-bodied organisms (Tucker 1970), in organisms with better developed locomotor system (e.g. Betts & Wootton 1988; Ducatez *et al*. 2012) or in organisms with higher body reserves or with a larger diet breadth, facilitating *en route* fuelling (Bowler & Benton 2005). Consequently, we expect to observe a positive association of dispersal rates and distances with body size, body condition, locomotor apparatus development, diet breadth and longevity. Notice, however, that some locomotor performances decay with body size for the largest species (Emerson 1978; Marden 1994; Maina 2000), which may result in bell-shaped dispersal-body size syndrome. Cost-reducing mechanisms might themselves be selected for the benefit they provide to organisms in other contexts than dispersal. We therefore hypothesise that a positive association between dispersal and other traits requiring low-cost movements and good navigation skills, like migration, will be evident. Contrasting environments can also select for contrasting navigation and motion capacities and hence contrasting dispersal costs: we thus hypothesise that dispersal rates and distances will vary according to habitat type and configuration.

These many working hypotheses make it difficult to predict unambiguously the strength and shape of dispersal syndromes. Moreover, complex trade-offs and feedback between traits are expected, which may blur the observation of dispersal syndromes. Our meta-analysis attempts to identify, for the first time, major patterns of inherently complex dispersal syndromes across a large number of species and taxonomic groups.

Genetic correlation among traits is a fifth possible mechanism causing dispersal syndromes across species, but was not used to build specific hypotheses as there are currently insufficient data to allow precise predictions on which traits might covary with dispersal and because, so far (1) the genetic architecture responsible for such covariation is still unknown and (2) genetic correlations can emerge from the evolutionary dynamics of trait relationships.

MATERIAL AND METHODS

Taxonomic coverage

To test our working hypotheses and characterise dispersal syndromes within and across taxonomic Orders, we created a unique meta-data set by integrating several pre-existing independent data sets on dispersal and other species traits. The criteria used to select the species included in our analysis are detailed in Appendix S1. Our selection retained terrestrial or semi-terrestrial animals, including mammals (Le Galliard *et al*. 2012b; Whitmee & Orme 2013), birds (Böhning-Gaese *et al*. 1998; Paradis *et al*. 1998; Dawideit *et al*. 2009), amphibians (Smith & Green 2005; JC, VMS & AT unpublished material), spiders (Bonte *et al*. 2003; Entling *et al*. 2011), dragonflies and damselflies (Harabis & Dolny 2011; Grewe *et al*. 2013), beetles (Turin 1999) and butterflies (Stevens *et al*. 2010b, 2012). Altogether, we considered 740 species belonging to 15 Orders (see Appendix S1 for data availability). These species have contrasting modes of thermoregulation: 596 use ectothermy and 144 use endothermy. They also use two different modes of locomotion (ground or aerial): a total of 255 species disperse by walking or jumping on the ground, and the remaining 485 species use aerial dispersal, including 76 species (the majority of the spiders) by ballooning with silk thread, and the remaining (409 bird and insect species) by active flapping flight. Species also vary in their trophic levels: 408 species are mainly carnivore or insectivore (grouped together for the purpose of our analyses), 193 species are herbivores, and 73 species have an omnivorous diet. Diet information was not available for 66 beetle species. Although amphibians primarily eat algae or plant material at the larval (aquatic) stage, they are strictly carnivorous at the terrestrial stage. As dispersal occurs primarily in terrestrial stage, amphibians were categorised as carnivores. The three characteristics (locomotion, thermoregulation and trophic level) were not correlated with each other at the species level (all $P > 0.08$).

Dispersal data

Dispersal is a movement of individuals or propagules that can result in gene flow (Ronce 2007). Here, we considered only active dispersal, i.e. a behaviour involving a decision to disperse, and we restricted our analysis to natal dispersal rather than breeding dispersal (dispersal between consecutive breeding events). We did not consider trans-generational dispersal data, such as the production of dispersing offspring or the colonisation success, because these measurements were rarely available for taxa with active dispersal. The way active dispersal is measured depends to some extent upon methodological constraints, but some standard methods exist, e.g. mark-recapture studies, radio tracking, and the study of genetic structure across a landscape. We thus used five dispersal measurements (see definition in Appendix S4) that are commonly quantified in several taxa. We considered the 'dispersal frequency', the fraction of individuals that leave their natal habitat patch or that initiate specific dispersal behaviour; the 'moment of dispersal distance' that is either the mean or the median of the dispersal distances obtained from mark-recapture surveys or from tracking; the 'maximum dispersal distance' recorded using mark-recapture or tracking; and the 'gene flow' estimated as 1-F_{ST}, with F_{ST} estimated at a landscape scale. F_{ST} depends on demographic and selective processes, while other genetic measurements like the isolation by distance can be more directly related to dispersal. However, F_{ST} is the most frequently reported index of genetic structure, while isolation by distance is only scarcely reported. Finally, we considered 'expert' scores of dispersal ability. Generally, a single value was reported by species and measurement; otherwise, we retained the mean value per species except for gene flow where we used the maximal value. The scale and duration of the study can influence quantitative estimates of dispersal (e.g. Le Galliard *et al.* 2012b). This bias could not be controlled here as data were pooled at the species level and not all methodological data were available. Strict quality control was, however, applied by the authors of the original data sets to avoid including biased data. Dispersal data are described in Appendix S1.

Trait data

From the working hypotheses developed above, we gathered data for 23 traits hypothesised as pertinent to the identification of dispersal syndromes. The traits studied are presented in detail for each taxonomic group in Appendix S1, and are listed in Table 1 where we summarise predictions about their covariation with dispersal. To better understand how dispersal syndromes may vary across the taxa, we used the following descriptors of species lifestyles: the mode of thermoregulation (endotherm or ectotherm), the mode of locomotion (ground vs. aerial) and the trophic level (carnivore [including insectivores], herbivore or omnivore depending on the main diet of the species). To describe the diversity of the last two characteristics at the level of Orders, we used the proportion of species with aerial dispersal (%aerial), the proportion of omnivorous species (%omnivore) and the proportion of herbivore species among non-omnivorous species (ratio of herbivores: the number of herbivores divided by the sum of herbivores and carnivore species). Variables %omnivore and ratio of herbivores described independently the variety of trophic levels in the Order.

Statistical analyses

Analysis of the phylogenetic signal

The phylogenetic signal of dispersal was measured separately for each of 9 Orders with > 15 species, and within each

Table 1 Species phenotypic traits used in the study. Numbers refer to mechanisms described in Fig. 1

Category	Trait	Brief description	Expected syndrome
Morphology	Body length	Log-transformed adult body length	Positive (4) or bell-shaped (4)
	Body mass	Log-transformed adult body mass	Positive (4) or bell-shaped (4)
	Body Mass Index	Measure of body condition: ratio of body mass to squared body length	Positive (4)
	Locomotor apparatus	Development of the locomotor apparatus relative to total body size	Positive (4)
Demography	Fecundity	Daily fecundity of females	Negative (2) or positive (1, 4)
	Survival	Survival expressed on a per-day basis from birth or metamorphosis	Negative (1), or positive (4) or bell-shaped (4)
	Age at maturity	Age at maturity in days, since birth or last metamorphosis	Negative (1)
Generalism	Habitat breadth	Number of different habitat types used	Positive (3), or U-shaped (3)
	Diet breadth	Breadth of the food resources	Positive (3,4), or U-shaped (3)
	Niche breadth	Breadth of the niche, or of a particular axis of the niche (shading, humidity and temperature)	Positive (3,4), or U-shaped (3)
	Circadian generalism	Absence of clear circadian specialisation	Positive (4)
	Seasonal generalism	Absence of clear seasonal specialisation	Positive (4)
Behaviours	Mate searching	Activity (intensity of movements) invested in mate searching	Negative (2) or positive (4)
	Foraging	Activity (intensity of movements) invested in foraging	Negative (2) or positive (4)
	Web building	Energy and time invested in web building	Negative (2) or positive (4)
	Parental care	Presence or intensity of parental care	Negative (2,3), or positive (4)
	Migration	Expressed as a binary trait: migrates or not, migration being here defined as to and fro periodic movements aiming at tracking suitable conditions	Positive (4)
Ecology	Habitat fragmentation	Typical level of fragmentation of the habitat used by the species (only available for spiders)	Positive (distance) and negative (rate) (4)
	Habitat type	Category of habitat used	Differences (4)
	Circadian rhythm	Diurnal/nocturnal/both	Dependent on locomotion mode (4)

Order for each dispersal measurement (18 measures, see Table A2 in Appendix S1). Several statistics can be used to quantify the phylogenetic signal (see a review in Münkemüller *et al.* 2012). In a preliminary investigation, we found that Blomberg's K (Blomberg *et al.* 2003), Pagels's λ (Pagel 1999) and Geary's statistic (Geary 1954) provided similar results and were highly correlated. We thus used here only Blomberg's K, as it allows the comparison among different phylogenies for continuous traits, across traits and tree types (Blomberg *et al.* 2003; Münkemüller *et al.* 2012). In a nutshell, if the resemblance of species in the trait of interest is due to the degree of shared evolutionary history, K should be 1; on the contrary, a small K value (close to zero) implies that close relatives resemble each other less in the trait of interest than is expected under the hypothesis of Brownian motion evolution along the phylogenetic tree. Overdispersion in trait expression may be due to adaptive evolution or to high measurement errors in the trait or in the construction of the tree (Blomberg *et al.* 2003). Blomberg's K statistic and associated *P*-values were calculated for each combination of Order and dispersal measurement types using the phylosignal function of the picante package in R (Kembel *et al.* 2010). Phylogenies are presented in Appendix S1. To check similarities in phylogenetic signal between different dispersal measurements and between taxa with different lifestyles, we fitted a linear model on K with additive fixed effects of thermoregulation, %flying, %omnivore, herbivore_ratio, number of species and dispersal measurement. We then selected among the fixed terms of this model by comparing the AIC of all the simpler models nested within it. Then, the best supported models (with $\Delta AIC < 2$ from the model with lowest AIC) were averaged using the model.avg function of the MuMIn R-package (Barton 2013).

Dispersal allometry

We modelled each dispersal measurement across the 740 species of the data set with a phylogenetic generalised least square (PGLS) in which the strength of the phylogenetic constraint (λ) was fitted by maximum likelihood (function pgls, R-package caper: Orme *et al.* 2012; see Appendix S2). A composite phylogeny that connects all taxa was built from the combination of the phylogenies listed in Appendix S1 according to the topology of Orders in the Tree of Life project (Maddison & Schulz 2007). Three different branch lengths were computed for this composite phylogeny: the tree called 'unity' had all branch lengths equal to 1; the tree called 'deep branches' had branch lengths of 1–24 for the branching of Orders (depending on the number of nodes on the corresponding part of the Tree of Life) and of 10^{-3} within each Order; and the tree called 'Grafen' had branch lengths computed according to the method developed by Grafen (1989) with power (rho) set to 1. In case λ did not significantly depart from zero with all trees, the PGLS was replaced by a linear model to avoid introducing potential biases due to uncertainty in phylogenies. Before selection (see Appendix S2), the model used to investigate dispersal–body size relationships was: response ~ (body size + body size^2)*(thermoregulation + locomotion + trophic). Given the data availability (Appendix S1) it was possible to conduct this analysis with response being either maximum dispersal distances or the moment of dispersal distances. Body size was either body mass or body length (both log-transformed). The quadratic term for body size (and its interactions with covariates) was retained conditionally of the presence of the linear term for body size and interaction terms.

Identification of dispersal syndromes within each Order

As dispersal was measured by a variety of methods and traits have different units, all trait and dispersal data were standardised for each Order by dispersal measurement. Standardised dispersal was called 'dispersiveness' (see Appendix S4) and can take several values for a given species if several dispersal measurements were available. Dispersiveness data were available for 740 species (955 estimates, mean = 1.3 per species, range = 1–4). We quantified the relationships between dispersiveness and each trait in each case (Order by dispersal measurement combination) using PGLS. We did this analysis for Orders with > 15 species available (i.e. 709 species of 9 Orders: see Appendix S1). We modelled a quadratic effect of the trait, and λ, the phylogenetic constraint, was fitted by maximum likelihood. We removed the quadratic term in cases where it was not significant, and we replaced the PGLS by a linear model when λ did not significantly differ from zero.

Generality of the dispersal syndromes across Orders

To analyse consistency in dispersal syndromes, we quantified the variation in effect sizes of dispersal syndromes using random-effects meta-regressions (Berkey *et al.* 1995) as implemented in the metafor R-package (Viechtbauer 2010). To limit variation due to differences in the methods used to extract effect sizes, we characterised dispersal syndromes using a PGLS with λ fitted by maximum likelihood including both linear and quadratic effects of the trait. Each dispersal syndrome was then summarised by the estimate and the corresponding standard error of the linear (β_1) and quadratic (β_2) slope of the standardised quadratic regression. Thus, β_1 and β_2 can be compared across cases (taxa and dispersal measurements) as we standardised trait values. Random-effects meta-regression was run separately for β_1 and for β_2 for ten syndromes, including the relationship between dispersiveness and Body Mass Index (BMI), locomotor apparatus, survival, fecundity, maturity, diet breadth, habitat breadth, migration, parental care and a composite of all measures of species' generalism. The low number of cases (8–33 per syndrome) precluded the integration of case-level moderators in the meta-regression, such as the lifestyle of the Orders. The analysis of factors causing variation in dispersal syndromes was thus addressed at the species level (see below).

Differences in dispersal syndromes according to species characteristics

To identify effects of lifestyles on dispersal syndromes, we analysed the covariation between dispersiveness and species traits, including fecundity, survival, maturity, BMI, locomotor apparatus, diet breadth, habitat breadth or migration across lifestyles. For that, we built one linear mixed model per dispersal syndrome: dispersiveness ~ trait*(thermoregulation + locomotion + trophic) + 1|Order. Models included a random deviation of the intercept among Orders to account for the group structure in the data. For dispersal syndromes with fecundity, survival and age at maturity, we included linear and quadratic effects of body length as demographic traits may covary with body size among species and body length data are available for more species than body mass data (Table A2 in Appendix S1). The linear effect of body length was included to scale out its effect even if weak and the quadratic term was subject to model selection (see Appendix S2). For the dispersal-locomotor apparatus syndrome, we did not include spiders and butterflies because their locomotor apparatus was not comparable to that of the other taxa (see Appendix S1). For the identification of dispersal syndromes, we did not consider the covariation due to phylogenetic relatedness as most syndromes were not constrained by phylogeny at the Order level (see results). Appendix S2 gives details on model selection procedures and *post hoc* tests.

RESULTS

Phylogenetic signal on dispersal

The strength of the phylogenetic signal for dispersal measured using Blomberg's K averaged 0.23 (± 0.16 SD). It was significantly different from zero ($P \leq 0.05$) in 10 cases out of 18, where it varied between 0.03 and 0.58 (average = 0.28 ± 0.16 SD). Blomberg's K did not vary significantly among dispersal measurements, but did vary among Orders with different modes of locomotion ($Z = 0.94$, $P = 0.004$). Blomberg's K was higher when the proportions of species with aerial dispersal increased (estimate ± SE: $0.0022 \pm 7 \times 10^{-4}$; Fig. 2). Blomberg's K was independent of thermoregulation mode, trophic levels of the Order, dispersal measurement and number of species, although the averaged model retained a non-significant trend of the number of species (estimate ± SE: $-0.0010 \pm 7 \times 10^{-4}$; $Z = 0.34$, $P = 0.156$) and of ratio of herbivores (estimate ± SE: $0.0001 \pm 7 \times 10^{-4}$; $Z = 1.30$, $P = 0.192$).

Dispersal allometry

Both maximum dispersal distance and the moment of dispersal distance scaled with species body size (Fig. 3). The effect of body length on the moment of dispersal distance was best modelled by a second-order polynomial without the inclusion of phylogenetic information (Table 2). The quadratic relationship was contrasted among species of different trophic levels (Fig. 3a). For carnivores and herbivores, the moment of dispersal distance increased with body length for species smaller than ca. 200 mm and then plateaued for larger species. The pattern differed for omnivores, whose moment of dispersal distance increased with body length, even for the largest species (Fig. 3a). *Post hoc* tests show that a linear increase of the moment of dispersal distance with body size is better supported than a quadratic relationship in omnivores (see Appendix S2). In this data set, only mammal and bird species had body length > 200 mm. A similar pattern linked mean and median dispersal distances to body mass, where, in addition, the relationship was influenced by the locomotion mode and was constrained by phylogeny (Fig. 3b; Table 2). By contrast, maximum dispersal distance was best predicted by a positive, linear model including either body mass (Fig. 3c) or body length (Fig. 3d), together with the interactions with trophic level and thermoregulation and phylogenetic constraints (Table 2). The effect of locomotion could not be tested here due to the absence of species with aerial dispersal in the subset of the data. Slopes for body size were steeper for herbivores and omnivores compared with carnivores (Fig. 3c and d). A significant difference in the allometry of maximum dispersal distance was also identified between ectotherms and endotherms: at similar mass or length, endotherms had longer maximum dispersal distances than ectotherms. It should be noted that all ectotherms in this subset were amphibians.

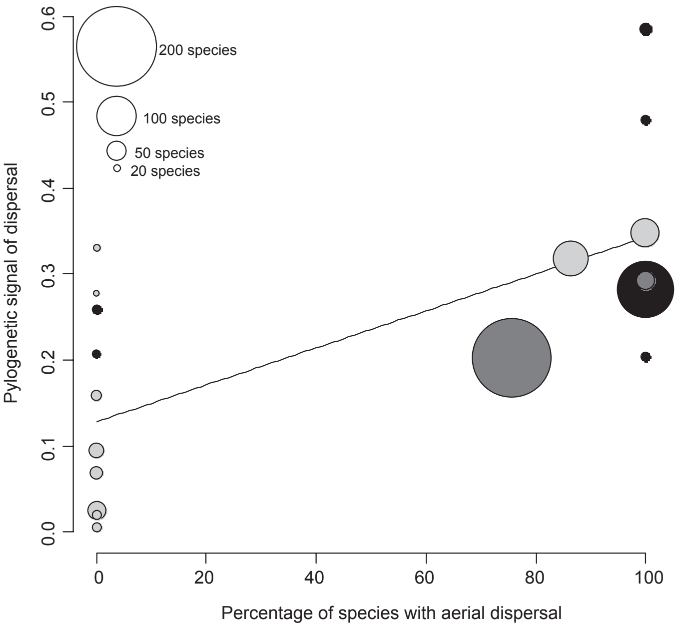

Fig. 2 Strength of the phylogenetic signal on dispersal, measured by Blomberg's K statistic at the taxonomic level of Orders and separately for each dispersal measurement, across a gradient of locomotion modes (proportion of species with aerial dispersal). Line illustrates the significant effect of locomotion mode. Symbol size is proportional to the number of species and grey scale illustrates the ratio of herbivore to non-omnivore species in the Order, two non-significant terms of the model retained to explain variation in phylogenetic signal (detailed in Table B1 of Appendix S2).

Dispersal syndromes within each Order

We investigated 161 syndromes linking one dispersal measurement to a trait. Sixty-seven of these cases revealed significant dispersal–trait relationships, among which 31 syndromes (of 67) were constrained by phylogeny, with λ ranging 0.18–1.00 (Fig. 4). Dispersal syndromes are less often phylogenetically constrained in ground-dispersing Orders (mammals and amphibians: 4/27 vs. birds and invertebrates: 27/40 syndromes). Syndromes were generally linear relationships, with quadratic relationships for only 20/67 syndromes. Meta-regressions confirmed the existence of a positive, linear association

Table 2 Best supported statistical models describing dispersal allometry for the moment of dispersal distance (mean or median) and for maximum dispersal distance. We assessed separately allometry for species log-body length (BL) and species log-body mass (BM)

Dispersal measure	Allometry	Model†	Phylogeny‡	Terms selected	F	ndf-ddf	Adj.R²	*P*-value
Moment	Body length	LM	None ($\lambda = 0$) §	Quadratic effect of BL Interaction with trophic level	9.505	8-183	0.263	<0.001
	Body mass	PGLS	Deep branches ($\lambda = 0.533$; IC = 0.001-0.862)	Quadratic effect of BM Interaction with trophic level Interaction with locomotion mode	2.176	12-146	0.076	0.016
Maximum	Body length	PGLS	Unity ($\lambda = 0.614$; IC = 0.313-0.836)	Linear effect of BL Interaction with trophic level Interaction with thermoregulation	9.922	8-162	0.223	<0.001
	Body mass	PGLS	Unity ($\lambda = 0.524$; IC = 0.225-0.779)	Linear effect of BM Interaction with trophic level Interaction with thermoregulation	8.944	8-141	0.273	<0.001

†Best models were selected in a set of linear models (LM) in which species are considered independent data points, and phylogenetic generalised least squares models (PGLS) in which a matrix of covariance depicts the interdependency of species due to common ancestry. See Appendix S2.

‡For PGLS, three composite phylogenies were tested that differed in their branch lengths. See Methods section.

§λ scales the phylogenetic constraint in PGLS and IC gives the 95% confidence interval. See Methods section.

between dispersiveness and survival, habitat breadth, generalism and migration (Table 3).

Dispersal syndromes across species

Some of the dispersal syndromes did not occur randomly across species (see details in Table B3 and Table B4 from Appendix S2). Higher dispersiveness is associated with greater BMI and in species with aerial dispersal, with longer locomotor apparatus relative to body size (Fig. 5d; Appendix S2). We also detected significant relationships between dispersiveness and the three demographic traits independently from the effect of body size on dispersal. The positive fecundity-dispersal and survival-dispersal syndromes were not affected by species lifestyles (Fig. 5a, c) while the negative relationship between dispersal and age at maturity was only detected among species with aerial locomotion (Fig. 5b). We found no significant relationship between dispersal and diet breadth. The relationship between dispersiveness and habitat breadth varied according to thermoregulation mode: this syndrome changed from close to zero in endotherms to significantly positive in ectotherms (Fig. 5e). Finally, dispersiveness was higher in migratory than in sedentary species, but only for flying and/or ectotherm species (Fig. 5f).

DISCUSSION

Origin of dispersal syndromes

Ronce & Clobert (2012) proposed that five mechanisms could be responsible for the evolution of dispersal syndromes. We were able to propose working hypotheses on the relationship between dispersal and phenotypic traits for four of them. Our analysis provides some support for three of these four mechanisms. A *parallel evolution of multiple traits* (path 1 in Fig. 1) was supported by the existence of a syndrome associating dispersal and early maturation and longevity. *The impact of dispersal on the evolution of another phenotypic trait* (path 3 in Fig. 1) may drive a relationship between dispersal and species propensity towards ecological specialism or generalism. The mirror mechanism, i.e. *the impact of the evolution of phenotypic traits on dispersal* (path 4 in Fig. 1), was also well supported: high dispersal ability may have evolved via reduced dispersal costs in migratory species and in species with higher BMI or longer flight apparatus. We found less support for a *common response of two traits to the environment* (path 2 in Fig. 1), from which we predicted several trade-offs to occur, including the dispersal–parental care trade-off observed in anurans that can also result from other mechanisms (Table 1). This mechanism is thus less likely to cause syndromes at the level of species, which does not preclude its potential to cause syndromes at the levels of populations or individuals. Even if a direct inference of evolutionary processes from the observation of phylogenetic patterns is risky, our analysis thus confirms the complex nature and multiple origins of dispersal syndromes.

Are dispersal syndromes universal?

There are several fundamental eco-evolutionary constraints leading to dispersal syndromes among a variety of taxa, and it is possible that these are not conserved, but instead have evolved multiple times. Very different evolutionary groups may thus converge on syndromes as a result of certain constraints. However, not all dispersal syndromes were universal across the 740 species of the data set because taxonomic attributes such as locomotion, thermoregulation and trophic level affected some of the dispersal syndromes. Trophic level influenced the dispersal-body size allometry (see next section), while locomotion and thermoregulation modes influenced both the dispersal-body size allometry and other syndromes. Some of these effects may be due to confounding factors as some lifestyles were represented by a single taxonomic group in our data set. Despite decades of work on dispersal, we thus still lack sufficient reliable, high-quality and representative estimates of dispersal in too many taxonomic groups to fully understand the factors structuring dispersal syndromes. Yet, the question remains about the respective role of the various mechanisms responsible for the evolution of dispersal syn-

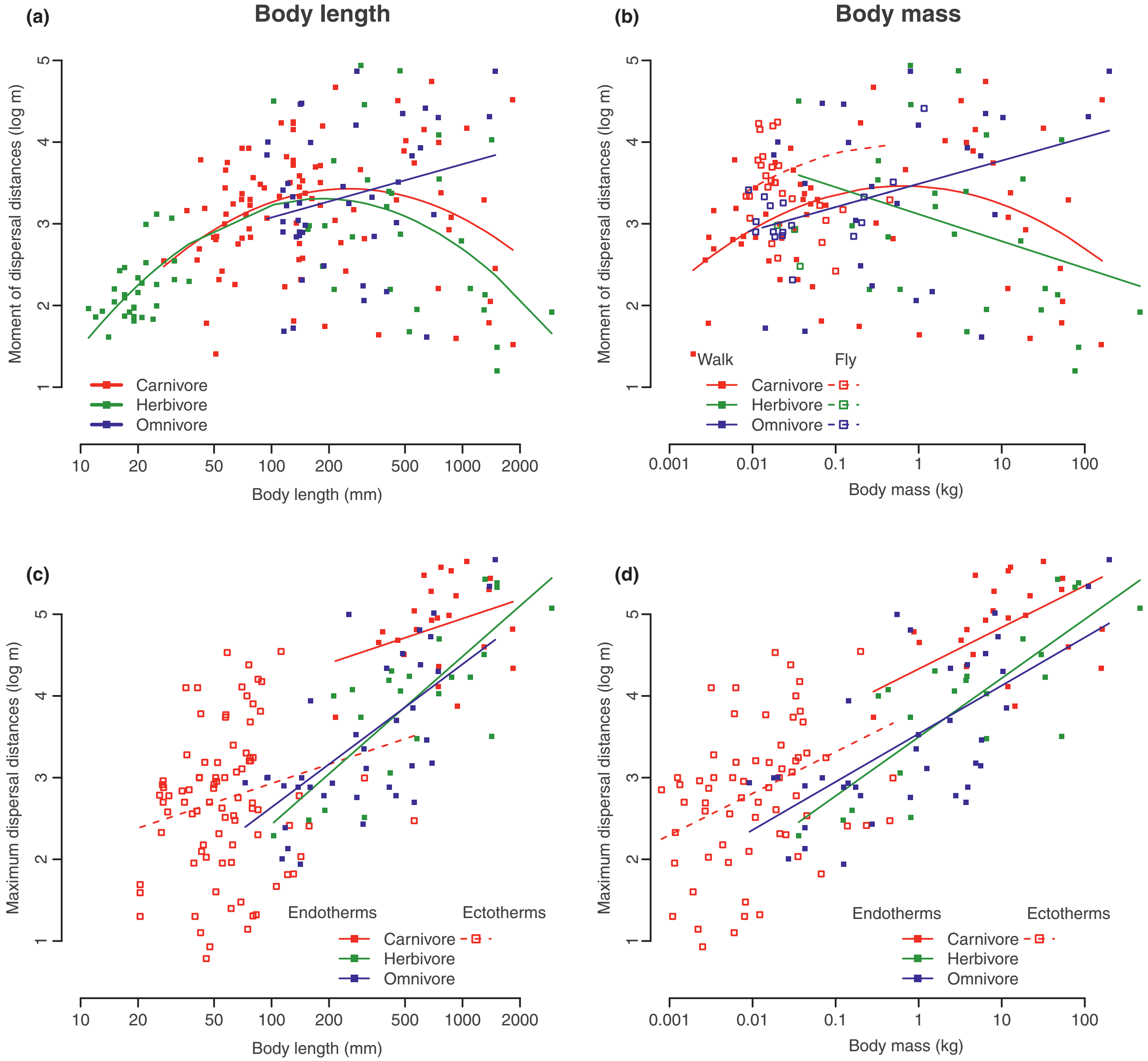

Fig. 3 Dispersal allometry across 740 terrestrial animal species belonging to 15 different Orders. The moment of dispersal distance (mean or median: a,b) and the maximum dispersal distance (c,d) plotted against either adult log-body length (a,c) or log-body mass (b,d). Lines show predictions for species with contrasted trophic level, thermoregulation and mode of locomotion obtained from *post hoc* models shown in Appendix S2. A version of this figure for colour-blind is available in Appendix S3.

dromes. Do similar syndromes appear in different taxa because a mechanism repeatedly led to the evolution of a common syndrome in different groups, or because different mechanisms led to syndrome convergence in different taxa?

Aerial locomotion is a crucial factor explaining taxonomic variation in dispersal patterns. The phylogenetic signal on dispersal and on dispersal syndromes was stronger for Orders with higher proportions of aerial species. Dispersal-migration, dispersal-maturity and dispersal-locomotor apparatus syndromes were also stronger for species with aerial dispersal than for ground dispersing species. Flight is a highly expensive activity in absolute terms (Maina 2000), but it is energetically more efficient compared with other modes of locomotion (Tucker 1970; Schmidt-Nielsen 1972): the cost of flight (per distance unit) for birds is approximately 30% of that of running for mammals with similar mass (Hainsworth 1981). This efficiency is possible thanks to profound adaptations of biochemical, physiological and morphological systems (Rayner 1981; Maina 2000). The evolution of flight has constrained the evolution of many life-history traits in birds (Gaillard *et al.* 1989; Roff & Fairbairn 2001). It is therefore not surprising to see that evolutionary history has a greater impact on this mode of dispersal than ground locomotion, which translates in higher phylogenetic signal and stronger associations of traits.

The mode of thermoregulation influenced the allometry between dispersal and body size and the syndrome between dispersal and habitat breadth, with stronger relationships in ectotherms than endotherms. For allometry, we observe an

Table 3 Results of meta-regressions on dispersal syndromes. Effect sizes are the coefficients of the linear (β_1) and quadratic (β_2) coefficient of the relationship between dispersiveness (standardised dispersal) and standardised trait value. Coefficients were obtained with phylogenetic generalised least squares (PGLS) quadratic regressions. Bold-typed cells show marginally significant ($P < 0.1$), significant ($P < 0.05$) or highly significant ($P < 0.01$) effect sizes.

		Effect size: β_1				Effect size: β_2			
Trait	# cases	Est.	95% CI	*Z*	*P*-value	Est.	95% CI	*Z*	*P*-value
Locomotor apparatus	8	0.137	−0.189; 0.464	0.82	0.411	−0.038	−0.306; −0.231	−0.27	0.784
Body mass index	11	0.113	−0.173; 0.399	0.78	0.438	0.002	−0.217; 0.221	0.02	0.987
Fecundity	17	0.069	−0.175; 0.316	0.55	0.558	0.017	−0.143; 0.177	0.21	0.835
Maturity	16	−0.055	−0.262; 0.153	−0.51	0.606	0.066	−0.093; 0.225	0.81	0.418
Survival	9	**0.501**	0.232; 0.770	3.65	<0.001	0.091	−0.099; 0.280	0.94	0.347
Generalism†	33	**0.223**	0.088; 0.357	3.26	0.001	−0.060	−0.189; 0.068	−0.92	0.356
Diet breadth	10	0.007	−0.269; 0.282	0.05	0.962	−0.049	−0.303; 0.206	−0.37	0.708
Habitat breadth	8	**0.264**	−0.004; 0.532	1.93	0.054	0.011	−0.250; 0.274	0.09	0.929
Migration	10	**0.297**	0.062; 0.531	2.48	0.013	NA	NA	NA	NA
Parental care	10	−0.014	−0.280; 0.252	−0.10	0.918	NA	NA	NA	NA

†Combined information from diet breadth, habitat breadth, niche breath (along up to three axes), circadian generalism and seasonal generalism.

increase of maximum dispersal distances with species body size with a higher intercept for endotherms than ectotherms. Peters (1983) calculated from physiological information the maximum distance for non-stop displacements of whole organisms of different mass and modes of thermoregulation. His calculation returned positive associations between mass and displacement for endotherms and ectotherms, but ectotherms were predicted to be able to perform longer non-stop displacements than endotherms of a similar size. Peters interpreted this as the result of higher basal metabolic rates in endotherms, and hence less available energy for their movement. We observed the contrary, which we tentatively interpret as the consequence of a taxonomic bias in our data. Maximum dispersal distance was available in our data set only for mammals and amphibians, thus implying a strong confounding effect of taxonomy on thermoregulation mode. Amphibians are highly sensitive to changes in air and soil moisture conditions, and this sensitivity might increase the costs of their movements through unfavourable habitats (Janin *et al*. 2012), reducing the distances they can reach as compared with mammals of similar sizes. Moreover, the difference in locomotion between mammals (fully erect locomotion) and amphibians (crawling or jumping) might explain part of the difference in their dispersal allometry.

Dispersal and body size

We found a linear syndrome associating dispersal with morphological attributes (body size, BMI and locomotor apparatus). It is not surprising that large species disperse farther, as this pattern was reported in several groups with contrasted modes of locomotion, including birds, mammals or fishes (Paradis *et al*. 1998; Sutherland *et al*. 2000; Bradbury *et al*. 2008). One potential explanation is that it is energetically less costly to move per unit mass and distance for large, mobile organisms than it is for small ones (Schmidt-Nielsen 1972; Hein *et al*. 2012). Yet, we also observed a quadratic relationship between body size and the moment of dispersal distances with evidence of lower dispersal distances in the largest species. This relationship may be explained by decay in locomotor performance with body size above a certain size threshold due to the inability of largest organisms to use some modalities of displacement (Emerson 1978; Marden 1994; Maina 2000). Alternatively, life-history variation may also contribute to explain this quadratic relationship. Species of greater dispersal ability tend to be the first to colonise new habitats where they benefit from a less competitive environment (e.g. Burton *et al*. 2010). At the same time, dispersal ability often trades off with competitive ability and survivorship, leading to a three-way interaction between body size, dispersal ability and demographic traits referred to as the 'competition–colonisation trade-off'. To go further in this issue, we suggest that dispersal should be considered explicitly within fitness equations that model the relationship between body size and life history (e.g. Roff 1986), and that the extra costs of dispersal in unfavourable conditions should be included in the physiological equations developed to predict the allometry of displacement to gain insights on this quadratic relationship between dispersal and body size.

Dispersal and life-history tactics

In evolutionary demography, dominant opinion is that life-history tactics are structured along a slow–fast continuum and dispersal covaries with this continuum because habitat instability promotes both the evolution of the fast tactic (by which both high fecundity and low survival permit fast population growth) and the evolution of high dispersal rates (Ronce & Clobert 2012). Such *a common response of multiple traits to the same environmental factor* might be responsible for the dispersal-age at maturity syndrome, as well as for the relationship between dispersal and fecundity. However, the selection for more dispersal under higher kin competition (i.e. path 4 in Fig. 1) might also be the cause for the observed dispersal-fecundity syndrome. Thus, *a single demographic trait can also influence selection on dispersal strategies* and potentially generate the (observed) positive dispersal-survival syndrome. The same syndrome (between dispersal and fecundity) can thus emerge from two different mechanisms, which illustrates here again the complex nature and multiple origins of dispersal syndromes. These results further confirmed our predictions that dispersal is an additional axis of life history, with a strong, universal association between high dispersiveness and high fecundity, but also a strong, positive association with survival rate, together with

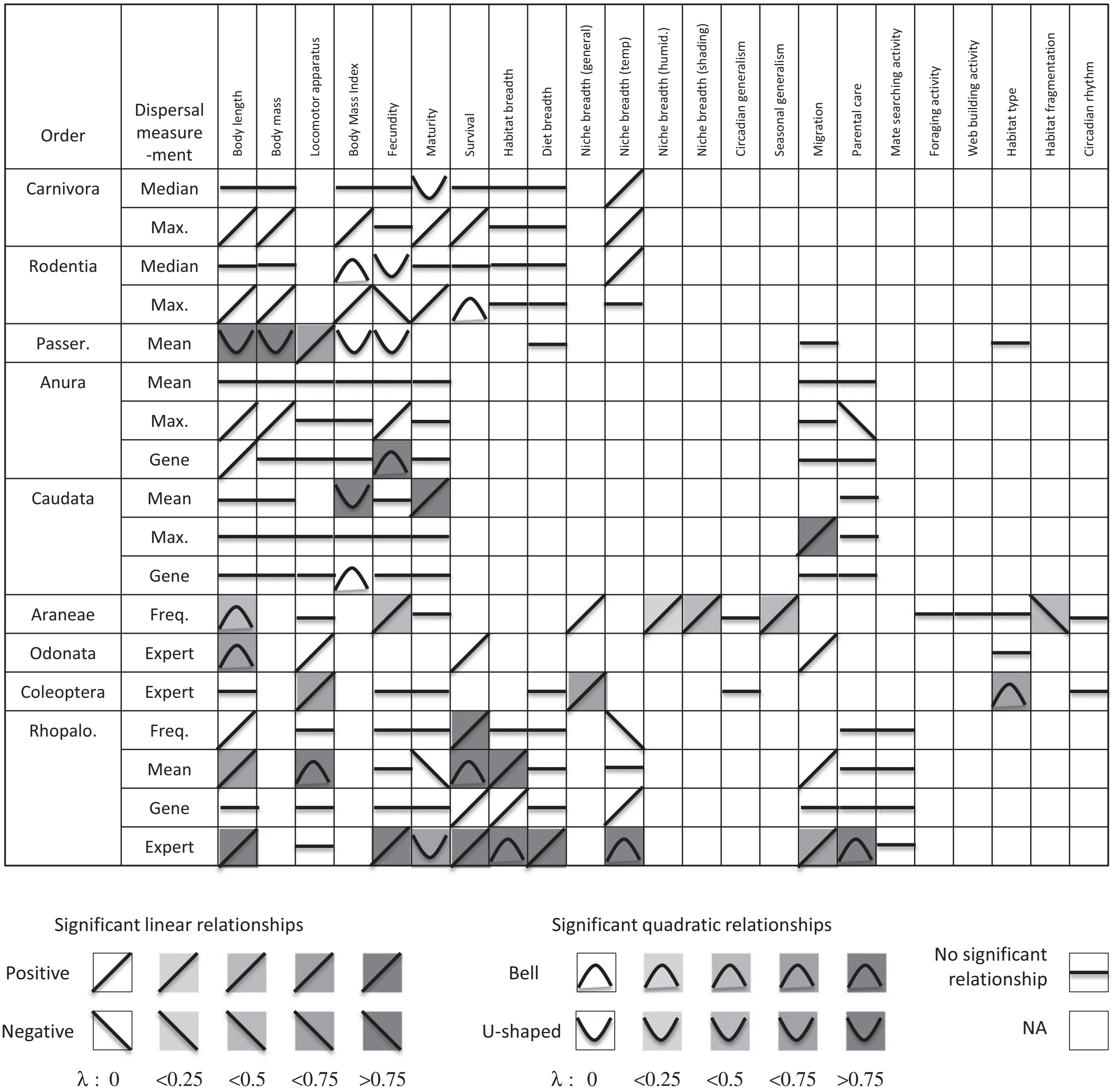

Fig. 4 Qualitative summary of the relationships between dispersal and other species traits across a variety of animal Orders. Dispersal was measured by expert scoring (Expert), gene flow among populations (Gene), the maximum (Max.) or the moment (Mean and Median) of dispersal distance, or the frequency (Freq.) of dispersal events. Traits are described in detail in Appendix S1. In each cell, the pictogram illustrates the relationship observed, with critical *P*-value for statistical significance set at 0.05 in each case. Background colour illustrates the strength of the phylogenetic constraint (λ), when significant.

variable relationships with age at maturity depending on the mode of locomotion. The exact pattern of correlation matched predictions from the life-history theory and empirical evidences: a recent review highlighted that selection either favoured the dispersal of individuals in space or advantaged life-history traits that distribute individuals into separate distributive events (Buoro & Carlson 2014). The life-history dispersal syndrome found here is also in line with predictions of models for metapopulations subject to extinction–colonisation dynamics in which competition, and particularly kin competition, promotes dispersal (e.g. Olivieri *et al.* 1995; Clobert *et al.* 2004). Dispersal thus has a pivotal role in the evolution of life-history tactics, by coupling the way by which organisms are able to manage simultaneously their use of space and time.

Consequences of dispersal syndromes for predicting species range shifts in a changing world

In principle, if dispersal allows a species to shift its distribution range at comparable rate than the global movement of its climate niche, stronger and longer dispersal should be beneficial for long-term species persistence in a changing

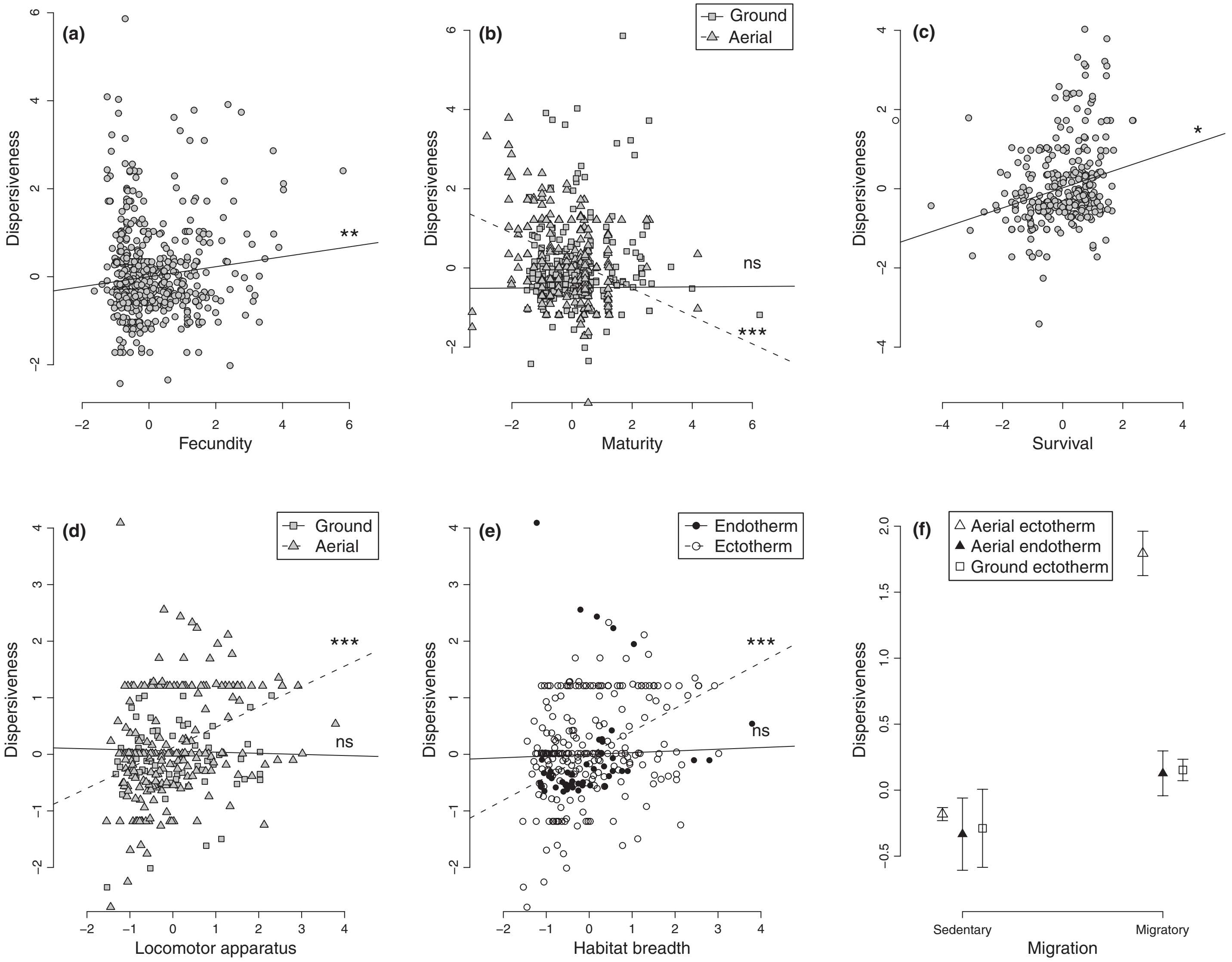

Fig. 5 Variation in dispersal syndromes of terrestrial animals between species traits and species groups. The syndrome between dispersiveness and six other species traits is shown separately for each group of species (see inset legends) according to the results of the best supported models summarised in Table B3 in Appendix S2. Life-history traits were standardised at the level of taxonomic Orders before calculations. Lines are predictions from the *post hoc* models shown in Table B4 in Appendix S2. NS: non-significant trend ($P > 0.10$); *, **, ***: significant effects ($P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively). A significant, positive relationship between dispersiveness and the Body Mass Index is not illustrated.

environment. Shifting range to stay within a moving climatic niche would preserve the fitness benefits provided by pre-adaptation to the climate (Feder *et al.* 2010). However, the benefits of co-migration depend also on population dynamics and on demographic traits of dispersers. For example, in taxa characterised by a flight–fecundity trade-off (e.g. Johnson 1969; Roff & Fairbairn 2001; Zera & Harshman 2009), species with sufficient dispersal ability for range shift would probably have low colonisation power. We show here that dispersal is in fact generally positively associated with fecundity, meaning that those species that have better dispersal capacities would also have the demographic potential to rapidly establish new populations at expanding fronts. High dispersal was also associated with better survival and higher longevity; this long life expectancy may help cope with sub-optimal habitat conditions at expanding fronts, and further improve species persistence. On the other hand, our analysis also showed that specialists have poor dispersal ability, implying that global climate change can be a double penalty for species with narrow tolerance, which will suffer more quickly and which will also be less likely to track the shifting environmental conditions.

Consequences for evolution in a changing world

Our meta-analysis of dispersal syndromes demonstrates the importance of multivariate selection on dispersal. Knowledge on the shape and strength of selection on dispersal is now particularly relevant because organisms are facing new selective pressures on dispersal due to habitat fragmentation (Baguette *et al.* 2012) and climate change (Le Galliard *et al.*

2012a; Travis *et al.* 2013). Habitat fragmentation, climate change and their interactions create new evolutionary pressures on dispersal behaviour by altering its cost–benefit balance (Kokko & Lopez-Sepulcre 2006; Berg *et al.* 2010; Le Galliard *et al.* 2012a; Baguette *et al.* 2013; Travis *et al.* 2013). Our results point to the fact that selection on dispersal could also entail the modification of phenotypic traits correlated with dispersal in a different manner depending on the lifestyle of the organism. More specifically, our analysis of dispersal syndromes indicates that a selective filtering on dispersal capacity will more likely incur side effects targeted to the distribution of traits related to specialisation or demography than of traits related to behaviour, and will more strongly affect flying taxa or ectotherms than ground dwellers and endotherms. Because dispersal and other traits are integrated into syndromes, particular values of covarying traits of many organisms could be positively or negatively selected in response to global changes. We suggest that the end product of this process could be the emergence or the extinction of particular dispersal-associated life-history strategies, causing cryptic changes in functional biodiversity within populations and communities.

CONCLUSION AND PERSPECTIVES

Our meta-analysis shows for the first time how dispersal and dispersal syndromes vary among taxa with very distinct lifestyles and morphology. We found differences in the phylogenetic signal of dispersal and in the shape of dispersal syndromes. Locomotion mode influenced dispersal-demography and dispersal-morphology syndromes, thermoregulation mode affected the dispersal-generalism syndrome as well as the allometry of dispersal distance, and trophic level was associated with differences in dispersal allometry. In herbivores and carnivores, a decay in dispersal ability was detected for the largest species. Dispersal syndromes were generally more pronounced for ectotherms and for flying species, while more variation existed for endotherms and ground dwellers. Even if the generality of our conclusions was sometime limited by the lack of data, our approach illuminates how current research on dispersal helps understand better the evolution of life histories and species interactions.

Future research on dispersal syndromes should attempt to challenge the conclusions we presented here by focusing on four major perspectives.

(1) The acquisition of high-quality data on more species remains a research priority. For instance, to better tease apart the respective roles of locomotion and thermoregulation, our analysis should be extended to swimming taxa, and should also include a larger number of endotherms with aerial dispersal (birds or bats). We also stress that a systematic report of isolation by distance, rather than F_{ST}-like information, would allow better understanding the syndromes associated with the different stages of the dispersal process (departure, transfer and settlement).

(2) The acquisition of additional data could help understand better sources of variation in dispersal syndromes. We were able to show that different dispersal syndromes exist across a wide variety of taxa with contrasted lifestyle, but future comparisons would be more informative if they can focus on species with similar lifestyle. For instance, a more stringent analysis of the relationship between dispersal and thermoregulation could be reached when more data on maximum dispersal distances of other ground-dwelling ectotherms, such as lizards, tortoises or other arthropods than those studied here will be available.

(3) We propose to define a new fitness dimension that we tentatively call lifetime dispersal effort, which could be measured like other fitness components using lifetime energetics, i.e. how individuals acquire and manage their energy all over their life. Using this dimension in simple life-history models, it should be possible to identify trade-offs in relative investment between dispersal and other fitness components (growth, sexual maturation, fecundity and survival), which should correspond to different dispersal strategies, and hence shape contrasted dispersal syndromes. This approach could, for instance, help identify and quantify how dispersal syndromes will emerge or get lost in the current era of global changes.

(4) The decline of the phylogenetic signal of dispersal with decreasing proportion of flying species is an important finding when thinking about community assembly structure. It indicates how temporal changes in phenotypic and phylogenetic diversities of communities would differ for organisms with different modes of locomotion. One may indeed expect that due to (1) the predominance of good dispersers at the early stages of succession and (2) the high phylogenetic signal of dispersal in flight capable taxa, the phylogenetic clustering of communities in newly colonised habitats should be higher for flying organisms than for ground dwellers. This scenario offers interesting perspectives for the design of biodiversity management strategies. In particular, the implementation of the linkage strategy aiming at (re)connecting similar habitats within heavily man-modified landscapes should be carefully thought according to this finding.

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AUTHORSHIP

Virginie M. Stevens and Michel Baguette designed the study and drafted the paper, with Jean-François Le Galliard. Sarah Whitmee, Jean-François Le Galliard, Jean Clobert, Michel Baguette & Virginie M. Stevens designed analyses with inputs of other authors, which were performed by Virginie M. Stevens and Sarah Whitmee. Katrin Böhning-Gaese, Dries Bonte, Martin Brändle, Jean Clobert, D. Matthias Dehling, Christian Hof, Audrey Trochet, Sarah Whitmee, Virginie M. Stevens and Michel Baguette provided the data. All authors substantially participated to the discussion of the results, read and approved the final version of the paper.

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