bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Dispersal: a central trait in life history

Dries Bonte – Maxime Dahirel

Ghent University, Dept. Biology, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium

contact: dries.bonte@ugent.be

[key-words]
movement, population persistence, vital rates, strategies, phenotypic heterogeneity, eco-evolutionary dynamics

[word-count]
main text ~4000 words
Three figures

Abstract

The study of trade-offs among major life history components (age at maturity, lifespan and reproduction) allowed the development of a quantitative framework to understand how environmental variation shapes patterns of biodiversity among and within species.

Because every environment is inherently spatially structured, Individuals need to move within and among habitats to maximize fitness. Dispersal is often assumed to be tightly integrated into life histories, in particular within the fast-slow continuum of life-history variation, and this integration is used to explain many aspects of population and community dynamics. Evidence for a general, context-independent, integration of dispersal in life histories is however weak, and suggests that dispersal needs to be considered as a central and independent axis in individual life histories.

We synthesize theoretical and empirical evidence on the central role of dispersal and its evolutionary dynamics on the spatial distribution of ecological strategies and its impact on population spread, invasions and coexistence. By applying an optimality framework we show that the inclusion of dispersal as an independent dimension of life histories might substantially change our view on evolutionary trajectories in spatially structured environments.

Because changes in the spatial configuration of habitats affect the costs of movement and dispersal, adaptations to reduce these costs will increase phenotypic divergence among and within populations. This phenotypic heterogeneity is anticipated to further impact population and community dynamics.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Introduction

Survival, fecundity and age at maturity are life history traits that are tightly linked to population-level demography and growth rate (Stearns 1989, Clutton-Brock and Sheldon 2010). They are typically organized in strategies, thus correlated and linked by both genetic and environmental covariation (Stearns 1989, Lindström 1999). Variation in these traits can be neatly integrated into an analytical framework to predict population persistence using, depending on the underlying driving variable(s), either classical matrix models or Integral Projection Models (IPMs) (Caswell 1990, Merow et al. 2014).

The quantification of life-history strategies is fundamental to advance ecology towards a predictive science enabling reliable forecasting, especially in light of global change (Selwood et al. 2015). The incorporation of quantitative genetics in IPM has for instance made it an indispensable tool to explore causes and consequences of eco-evolutionary dynamics in (semi-) wild populations (Coulson 2012, Smallegange and Coulson 2013, Vindenes and Langangen 2015). When detailed individual-based life-history metrics are unavailable, species-specific estimates are used to infer the fate of populations under environmental change. For instance, Salguero-Gómez et al. (2016), expanding Stearns (1983)'s approach to plants, found for 418 plant species that life strategies could be synthesised by two principle axes representing respectively the pace of life (fast-slow continuum) and a wide range of reproductive strategies. The authors subsequently used this framework to predict species demographic responses to (anthropogenic) disturbances, and advocate its use to study species persistence in changing environments. Species traits linked to the fast-slow continuum were also found to influence extinction threat status in birds and fishes (Jeschke and Strayer 2008).

Dispersal is defined as any movement potentially leading to gene flow (Ronce 2007), so movements beyond what Addicott et al. (1987) defines as the ecological neighbourhood. This definition lends itself to an individual-centred view on dispersal as a trait affected by environmental, genetic, and physical constraints (Clobert et al. 2009, Bonte et al. 2012). Dispersal is a complex, multivariate trait involving several stages that eventually determine net displacement between locations of birth and subsequent reproduction. These stages comprise departure, transfer and settlement, and each of these stages is expected to be under selection so to reduce the overall costs of dispersal (Travis et al. 2012, Bonte et al. 2012). Dispersal is selected as a way to avoid competition with relatives, reduce the risks of inbreeding, or spread risk in spatially and temporally varying environments

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

(dispersal as an adaptation). The overall dispersal process may however be affected by other selective forces related to e.g. foraging or reproduction, rendering dispersal likely an important, but largely unintegrated trait in classical life history (dispersal as a by-product; see Van Dyck and Baguette 2005, Burgess et al. 2015).

Without dispersal, the fate of any population is extinction, whatever the survival rate and reproductive output of its constituent individuals. A life history-theory that includes dispersal is thus needed to understand the diversity of life forms on Earth and their dynamics in space and time. Several prominent theoretical frameworks aiming to explain both dispersal and classical life-histories tend to assume consistent and often genetically driven correlations between dispersal and classical life history traits (henceforth, "genetic integration" or "integration"). Such frameworks, which sometimes appear to contradict each other, are often invoked to explain spatial dynamics of species and traits. For instance, the metapopulation/metacommunity framework incorporating dispersal-competition trade-offs (Yu and Wilson 2001, Leibold et al. 2004, Calcagno et al. 2006) has fostered the view that dispersal should per definition be integrated into individual life histories through trade-offs with other vital traits, and that this integration explains community dynamics. Dispersal-reproduction trade-offs are often automatically assumed when developing models of dispersal evolution (Travis et al. 2012). Also at the individual level, dispersal is often considered integrated within the classical life-history fast-slow continuum, with "fast" organisms spreading more, an assumption that still prevails in current iterations of the pace of life concept (Réale et al. 2010). Organisms must become spatially dispersed as they grow, reproduce, and die, if they are to avoid density-dependence and maintain exponential growth (Holt 2009). Southwood (1977) developed in his seminal presidential address to the British Ecological Society a framework that integrated (stochastic) fitness expectations, dormancy and dispersal to understand the evolution of ecological strategies in relation to spatiotemporal dimensions of the habitat.

In this paper, we synthesise data and views on how dispersal is integrated into life histories. We show that evidence for a genetic integration is weak, and that its genetic basis is largely overruled by condition dependence, so plasticity. We plea to put dispersal independently central in life histories and discuss implications for our understanding of spatial eco-evolutionary dynamics.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Is dispersal genetically integrated in life histories?

Connections between dispersal and other traits are referred to as dispersal syndromes (Ronce et al. 2012). In animals, dispersal is typically integrated into life histories at the species-level through size dependency (Stearns 1983, Gaillard et al. 1989), but the relationship between dispersal and size is definitively not general, nor uniform among several taxa (Stevens et al. 2014). Most importantly, stronger evidence for dispersal-size correlations was found in aerial dispersers and ectotherms, relative to ground dwellers and endotherms. This suggests that dispersal becomes more integrated in species life histories in organisms that have specific adaptations for longer distance movements (i.e., wings). Such investments are often very costly from a developmental perspective and therefore trade-off with investments in reproduction or early-maturation. However, Stevens et al. (2014) analysed multiple measures of dispersal jointly (from data on genetic differentiation among populations to expert judgement), rendering a formal synthesis difficult to make as some measures are confounded by variation in habitat configuration or population sizes. In butterflies, classical life histories are good predictors of dispersal distance, but whether correlations between dispersal related and other life history traits results from genetic integration or from independent responses to common pressures remain unknown (Stevens et al. 2013, 2014). For plants, Thompson et al. (2002) did not find convincing evidence for trade-offs between seed dispersal and several demographic parameters. Seed mass and especially plant height did contribute most to dispersal distance (Thomson et al. 2011). Seed morphology is however a poor predictor of long-distance) dispersal because it is determined by multiple processes (several vectors, abiotic conditions) that move seeds (Higgins et al. 2003).

Like classical life history traits (Lindström 1999), dispersal is known to be context- and density dependent (Clobert et al. 2009, De Meester and Bonte 2010, Bitume et al. 2013, 2014) and thus highly heterogeneous when studied at the population level. An analysis of phenotypic data on dispersal and movement of European butterflies reveals at least as much variation within as among species (Stevens et al. 2010). At the individual level, dispersal –encompassing emigration, transfer and settlement- should always be optimised to maximise fitness under the prevailing environmental conditions (Bonte et al. 2014) although constraints due to other selection pressures might shape evolutionary trajectories in a non-adaptive manner (Burgess et al. 2015). This optimisation implies that consistent associations between traits and different dispersal phenotypes (including residents) might not exist and that they are likely to be context-dependent. Despite the general view of wing development-life history trade-offs in insects, Guerra (2011) found by meta-analysis that the strength and direction of the association

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

between wing dimorphism and life traits was quite heterogeneous. Only relationships with fecundity (flight-oogenesis syndrome) appeared to be overall strong, and even then some insect orders (e.g. Coleoptera) consistently present the opposite of the "canonical" trade-off pattern. While wing development should not per se be related to dispersal, any absence of wings must impair the dispersal process. In species lacking such obvious polymorphism, evidence for consistent dispersal syndromes is less clear.

While numerous cases of within-species life history-dispersal syndromes have been reported, there is no consistency in the strength and sign of specific associations (Ronce et al. 2012). So far, few studies have gone beyond simple observations of phenotypic correlations and evaluated the genetic integration of dispersal in individual life histories. One reason is that such insights on genetic correlations can only be generated using model species under standardized breeding conditions and dispersal experiments, or with large life history datasets and deep enough pedigrees compiled in the course of long-term field studies. In existing studies, evidence for genetic integration is mixed (Clobert et al. 2009). Genetic correlations between wing morph expression and fecundity have been consistently found in several wing dimorphic cricket species (Roff 1994, Roff and Bradford 1996, Roff and Fairbarn 2011). By contrast, in the moth *Epiphyas postvittana*, the strength of genetic correlations between flight ability and lifespan/fecundity was highly variable between populations (Gu and Danthanarayana 1992). In the spider mite *Tetranychus urticae*, no genetic correlations were observed between aerial dispersal and fecundity (Li and Margolies 1994). In *Erigone* spiders and *Melitaea* butterflies, phenotypic correlations with vital rates were observed across different experimental or metapopulation contexts, pointing at the existence of colonization syndromes (Bonte and Saastamoinen 2012). In both species however, consistent correlations could not be detected. Figure 1 (data from Bonte et al. 2008) visualises the correlation of several dispersal proxies (in blue) with vital traits like reproductive output, reproduction, age at maturity and web building. Spiders were reared using a half-sib design at four different temperatures. Some dispersal proxies (activity and ballooning) correlated with age at maturity at the individual level when all treatments were combined. This correlation does, however, disappear when individual traits are studied within each temperature treatment (Fig 2). In *Melitaea*, the overall phenotypic correlations equally disappeared when mobility was tested under common garden conditions (Duplouy et al. 2013).

Although there is definitely a need to collect more data on the shape, strength and consistency of individual dispersal syndromes, the available theory on the joint evolution of dispersal and other traits largely confirm the

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

optimality of independently evolving dispersal-life traits correlations. Dytham and Travis (2006) allowed age-at-death to evolve jointly with emigration and found the cost of dispersal to strongly impact the joint and non-consistent evolution of both traits. Similarly, landscape dynamics, costs of dispersal, the level of environmental stochasticity affect both the strength and direction of dispersal-fecundity syndromes (Ronce et al. 2000, Bonte and de la Peña 2009). Evidently, when dispersal and other life traits are genetically linked, the shape of the trade-off function will affect the mutual evolutionary dynamics (Weigang and Kisdi 2015)

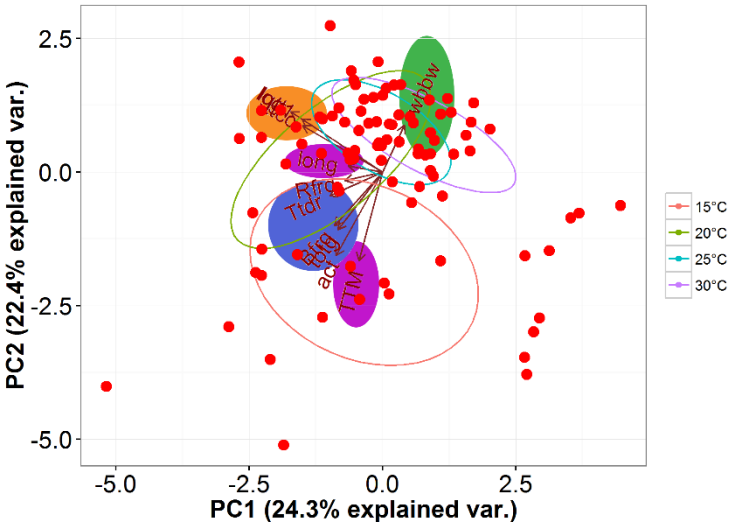

Fig 1. Organisation of spider life histories along principal components. The following traits were tested for sibs of Erigone atra *reared at four different temperatures during development conditions under laboratory conditions at the individual level: trait linked to dispersal (Ballooning frequency Bfrq, Rapelling frequency Rfrq, total duration of the tiptoe behaviour Ttdr, overall activity Act; in blue) time till maturity TTM or longevity LONG (in purple), webbuilding behaviour (green) and fecundity (total eggsacs ttcc, lifetime fecundity lgtt and eggs/eggsacs log1; in orange). Strategies are determined by the breeding temperature conditions (data from Bonte et al. 2008)*

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

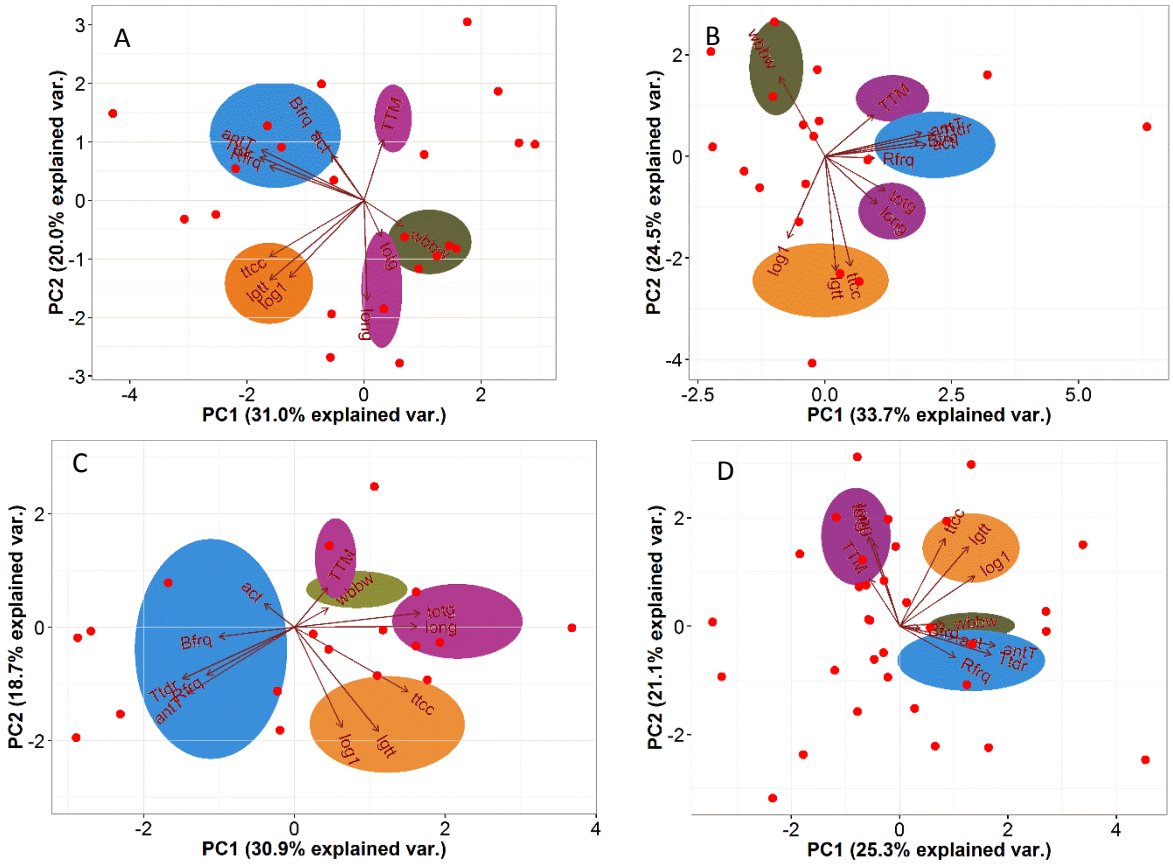

Fig 2. Traits related to dispersal are differently correlated with the overall life history contingent to the temperature of development (A: 15°C; B: 20°C; C:25°C; D: 30°C). The following traits were tested for female sibs Erigone atra *reared at four different temperatures during development conditions under laboratory conditions at the individual level: trait linked to dispersal (Ballooning frequency Bfrq, Rapelling frequency Rfrq, total duration of the tiptoe behaviour Ttdr, overall activity Act; in blue) time till maturity TTM or longevity LONG (in purple), webbuilding behaviour (green) and fecundity (total eggsacs ttcc, lifetime fecundity lgtt and eggs/eggsacs log1; in orange). Strategies are determined by the breeding temperature conditions (data from Bonte et al. 2008)*

Consequences - genetic basis and integration

Dispersal is not a side-product of "classical" life history trait evolution, or a simple trait linearly organised on the fast-slow continuum. The available data and theoretical insights so far point to dispersal being a central and independent life history trait, with impacts for both local and regional demography. A synthesis on the genetic basis of dispersal and its integration in life histories is unfortunately constrained by methodological and conceptual issues related to the diverse manners and scales of biological organisation it is measured. Any preconceived view of dispersal as an integral part of Malthusian growth rates or as deterministic integrated into the pace of life concept will further constrain the development of new insights in spatial (evolutionary) ecology.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

While genetic correlations with other traits are far from general, evidence on the genetic background of dispersal itself is compelling (Zera and Brisson 2012). It is therefore central to eco-evolutionary dynamics in metapopulations. Under the assumption that dispersal is only determined by genetic variation, any variance in fitness expectations among patches selects for dispersal till the level where an ideal free distribution is reached. Under such conditions, the evolution of dispersal will be relaxed until kin competition, inbreeding and demographic stochasticity become too strong. The balance between demographic variation, inbreeding and kin competition will thus maintain spatiotemporal variation in dispersal at the metapopulation-level. The close interaction between ecology and evolution in metapopulations has for instance been demonstrated in Glanville fritillary butterflies where dispersal and overall activity is determined by allelic variance in *PGI* among young and old islands populations (Hanski and Saccheri 2006, Klemme and Hanski 2009, Niitepõld et al. 2009, Niitepõld 2010, Hanski and Mononen 2011). These eco-evolutionary dynamics may not always, however, be strong enough to sustain population persistence, as similar signals of selection were witnessed in historical samples from now extinct (meta)populations (Fountain et al. 2016).

Dispersal is also selected during range expansion through spatial sorting (Shine et al. 2011). Here, asymmetric gene flow and assortative mating is predicted to speed-up range expansions. Depending on feedbacks with ecological (e.g., demography) and other evolutionary processes (e.g., the rate of local adaptation), eventual range dynamics may be either facilitated or constrained (Kubisch et al. 2014). As for metapopulation dynamics, integration of dispersal into life history will then lead to non-random dynamics of vital rates which theoretically affect further ecological and evolutionary processes (Burton et al. 2010). Individual-based models show for instance that dispersal evolution during range expansion can be constrained by investments in competitive abilities, reproduction (Burton et al. 2010) and thermal adaptations (Hillaert et al. 2015). While some studies demonstrated significant divergence in dispersal between range and core populations in expanding populations (Phillips et al. 2010, Therry et al. 2014a, b, Fronhofer and Altermatt 2015, Huang et al. 2015), only few demonstrated a genetic integration into broader behavioural strategies. Generally, dispersal and aggressiveness or boldness appeared to be coupled at range expansion fronts (Cote and Clobert 2007, Duckworth and Badyaev 2007, Cote et al. 2010, Korsten et al. 2013). However, and in line with earlier described expectations, a study combining quantitative genetics and inverse modelling demonstrated that dispersal and life history traits independently evolve according to respectively spatial sorting and local environmental conditions (Van Petegem

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

et al. 2016). It remains however to be studied to which degree evolved changes at range borders effectively affect ecological dynamics since environmental and demographic conditions may be highly different.

Convincing empirical evidence that dispersal is tightly and consistently correlated with classical life histories is lacking. This implies that we need to critically question the fundamental role of dispersal limitation as a determinant of trait and functional diversity dynamics during succession (Lortie et al. 2004). Under the assumption that dispersal and vital rates are decoupled at the species-level, colonisation dynamics will be more determined by propagule load –the regional abundance of certain species- and local filtering effects rather than by dispersal constraints *per se*. This view forces us subsequently to move away from a deterministic theory on community assembly, but to consider selection, stochasticity and contingency as the most important driving mechanisms (Vellend 2010, Vellend et al. 2014a, b). In such cases, spatial isolation rather than species-averaged dispersal traits will be a strong predictor of both local and regional trait variation. While experimental seed addition experiments (e.g., Pinto et al. 2014) highlighted the potential structuring role of dispersal limitation, inverse approaches linking trait diversity to local environment, isolation and mean and variance in dispersal traits will be highly informative to challenge current views on assembly rules in spatially structured systems that are in disequilibrium. A recent study on functional variation in island plant communities did not find a strong support for the role of dispersal in explaining trait variation associated with spatial isolation, despite a close association between functional traits and dispersal mode (Negoita et al. 2015). Obviously, firm inference of mechanisms driving community assembly is difficult to draw from pattern-oriented approaches. Using simulations of expanding finite populations, Williams et al. (2016) found that expected eco-evolutionary dynamics along expanding fronts may be highly dependent on the patchiness of landscapes and that the long-term outcome of evolution strongly depended on which strategy initially prevailed through a spatial priority effect. In the same vein, serial founder events and drift on the expanding range edge render evolutionary trajectories in the invasion vanguard highly stochastic and eventual ecological dynamics highly unpredictable (Phillips 2015). We thus advocate researchers to carefully select replicated systems that allow disentangling the respective role of determinism versus stochasticity and contingency as driving factors of community assembly.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Consequences - condition dependency

When drift and founder effects can render spatial processes highly stochastic, then to which extent can we generalise insights from the few studies that found significant covariation between dispersal and life traits, or from those reporting selection during range expansion? Indeed, even established dispersal syndromes have been shown to break down or reverse when tested in a different context (Guerra 2011, Cote et al. 2013). Similarly, while evidence on the genetic background of dispersal is strong, an equal share of work has demonstrated an overruling importance of plasticity and context dependency in many cases (Clobert et al. 2009). This implies that GxE interactions are rather rule than exception and that depending on the environmental conditions (density or predation pressure for instance), different syndromal associations emerge. More and more, we learn that elements such as transgenerational plasticity (Bitume et al. 2014, Van Petegem et al. 2015) or disease and more cryptic microbial interactions (Goodacre et al. 2009, Debeffe et al. 2014) may affect dispersal and its association with other vital traits. These insights further strengthen the case for leaving a deterministic view of spatial ecology, to embrace uncertainty and context-dependency. Such a view, however, should not imply that dispersal should be abandoned when studying mechanisms and patterns of spatial dynamics, but that its complexity should be better accounted for.

Philopatric and dispersing individuals likely differ in vital rates because optimality theory predicts that –when phenotypic variation is available- that individual decisions should match fitness prospects in respectively natal and new environments. In most simple cases these environments differ in demographic conditions (Cotto et al. 2014, Bonte et al. 2014), but they may alternatively differ more coarsely, for instance in habitat quality or typology (Edelaar et al. 2008, Tarwater and Beissinger 2012). The importance of phenotypic variation should not be underestimated and can strongly affect metapopulation and metacommunity processes (Shima et al. 2015, Jacob et al. 2015). Individual phenotypic variation in size contributed for instance more to population dynamics than environmental fluctuations in several mammal species (Ezard et al. 2009). Phenotypic correlates with body size were even demonstrated to impact population dynamics more strongly in receiver populations (Ozgul et al. 2010). These advantages can be directly related to enhanced competitive abilities to take-over various resources (e.g., Bonte et al. 2011) or abilities to deal with general stressors. Furthermore, and even more stochastically, released competition at founder patches relaxes density dependence, and may subsequently lead to monopolisation mechanisms that control population sizes, community assembly and evolutionary potential

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

(Urban and De Meester 2009, De Meester et al. 2016, Williams et al. 2016). Within a food web perspective, phenotypic variation has been demonstrated to affect interaction strengths between prey and predators (terHorst et al. 2010). Plasticity in traits may thus largely impact population and community dynamics (Miner et al. 2005). Except for some invasive species (Berg and Ellers 2010), we do, however, lack deep insights on its generality and context dependence. For dispersal dynamics in particular, carry-over effects across life stages (Van Allen and Bhavsar 2014) or even generations (Bitume et al. 2011, 2014) can be particularly relevant to maintain and generate spatiotemporal variation in demography among local populations (Benard and McCauley 2008).

Generally, emigration and immigration strategies need to be considered as threshold responses towards the local environment (context) or trait value (condition) (Clobert et al. 2009). The threshold value may be heritable and depicts the developmentally or environmentally determined condition at which individuals decide to switch behavioural states (Bonte and Lens 2007, Yan et al. 2014), in this case to leave or to settle (Fig. 3).

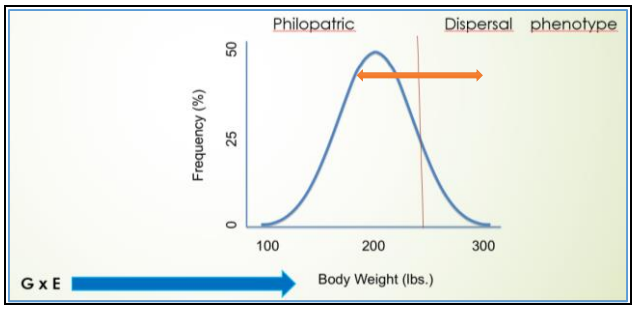

Fig. 3. The trait threshold model for dispersal. A population exhibits a substantial amount of phenotypic variation, here Gaussian distributed body weight as an example. Depending on the environmental conditions, density for instance, the threshold values (red line) for the phenotypic trait (determined by GxE) to switch between staying and leaving may shift to the right or left (red double arrow). The initial distribution is subsequently split into a divergent trait distribution of the philopatric and dispersive phenotype.

Theory predicts that different conditional dispersal strategies might evolve in response to metapopulation conditions (Bonte and de la Peña 2009, Gyllenberg et al. 2011, Kisdi et al. 2013). Based on similar optimality arguments, different phenotypes can be expected to be associated with dispersal when local environmental conditions are different, for instance in terms of density and relatedness. Just like stochastic switching strategies are advantageous in local fluctuating environments (Acar et al. 2008), adaptive dispersal phenotype switching should lead to metapopulation stabilisation. Conditional strategies are then additionally expected to lead to maintenance of genetic and phenotypic variation within metapopulations. Both genotypic variation and phenotypic dissimilarity need therefore to be considered collectively to better understand population performance (Ellers et al. 2011). Flexible floating strategies, where non-dispersive individuals contribute to

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

parental fitness through helping are another demonstration of how phenotype-dependent dispersal strategies eventually have an ecological impact beyond the individual (Cockburn 1998). Unsurprisingly, available evidence on the interplay between phenotype-dependent dispersal and demography comes from systems that allow manipulation of spatial structure, population dynamics and dispersal phenotype. By using a marine bryozoan as a model, Burgess and Marshall (2011) demonstrated interactive effects of colonizer phenotype and abundance on the reproductive yield of populations. In their study, populations established from a few individuals with short dispersal durations, which means better condition and potentially shorter distances, had similar reproductive yield than populations established by much higher number of founders that experienced long dispersal duration. In contrast, population biomass and recruitment were very influenced by colonizer abundance, but not colonizer phenotype. Context-dependent changes in disperser abundance and phenotype can thus lead to complex and poorly understood decoupling of demographic parameters. Finally, while habitat matching strategies may eventually maximise metapopulation performance and connectivity (Jacob et al. 2015), converse consequences are expected in environments where selection pressures vary over spatial scales such that phenotype–environment mismatches emerge. Such habitat mismatches can be expected in marine but also many terrestrial organisms and will eventually constrain connectivity (Marshall et al. 2010)

Conclusion

Fitness is maximised by the optimisation of life history strategies as classically determined by vital rates, i.e. survival and reproduction. Without dispersal though, any deme is doomed to go extinct. To date, dispersal is typically considered to be a tightly integrated trait into life history, either by its association with reproduction or survival. We here advocate that this assumption may hold at higher levels of biological organisation, but that at the individual level, dispersal actually needs to be considered as an independent axis in the multivariate life history trait space, with observed trait associations being largely context-and scale-dependent. We lack a general theory on how syndromal associations between dispersal and life history traits change according to local and metapopulation-level environmental conditions. This decoupling forces us to rethink the deterministic nature of spatial population and community processes. There is evidence that phenotypic variation in dispersal can alter ecological dynamics, but more experimental work is needed to develop a general theory on the role of dispersal for eco-evolutionary dynamics in space.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Acknowledgements

MD is a post-doctoral fellow funded by the Fyssen Foundation. DB acknowledges FWO research network EVENET and Belspo IAP 'SPEEDY' for funding and is grateful to the Nordic Oikos Society for the support to organise the thematic symposium. Scott Burgess and Denis Réale provided very valuable comments on an earlier draft version.

References

Acar, M. et al. 2008. Stochastic switching as a survival strategy in fluctuating environments. - Nat. Genet. 40: 471–475.

Addicott, J. F. et al. 1987. Ecological neighborhoods: scaling environmental patterns. - Oikos 49: 340–346.

Benard, M. F. and McCauley, S. J. 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. - Am. Nat. 171: 553–567.

Berg, M. P. and Ellers, J. 2010. Trait plasticity in species interactions: a driving force of community dynamics. - Evol. Ecol. 24: 617–629.

Bitume, E. V. et al. 2011. Heritability and artificial selection on ambulatory dispersal distance in tetranychus urticae: Effects of density and maternal effects. - PLoS One 6, e26927.

Bitume, E. V. et al. 2013. Density and genetic relatedness increase dispersal distance in a subsocial organism. - Ecol. Lett. 16: 430–437.

Bitume, E. V et al. 2014. Dispersal distance is influenced by parental and grand-parental density. - Proc. Biol. Sci. 281: 20141061.

Bonte, D. and Lens, L. 2007. Heritability of spider ballooning motivation under different wind velocities. - Evol. Ecol. Res. 9: 817–827.

Bonte, D. and de la Peña, E. 2009. Evolution of body condition-dependent dispersal in metapopulations. - J. Evol. Biol. 22: 1242–1251.

Bonte, D. and Saastamoinen, M. 2012. Dispersal syndromes in spiders and butterflies. - Dispersal Ecol. Evol.: 161–170.

Bonte, D. et al. 2008. Thermal conditions during juvenile development affect adult dispersal in a spider. - Proc. Natl. Acad. Sci. U. S. A. 105: 17000–17005.

Bonte, D. et al. 2011. Selective integration advantages when transience is costly: immigration behaviour in an agrobiont spider. - Anim. Behav. 81: 837–841.

Bonte, D. et al. 2012. Costs of dispersal. - Biol. Rev. 87: 290–312.

Bonte, D. et al. 2014. Fitness maximization by dispersal: evidence from an invasion experiment. - Ecology 95: 3104–3111.

Burgess, S. C. and Marshall, D. J. 2011. Are numbers enough? Colonizer phenotype and abundance interact to affect population dynamics. - J. Anim. Ecol. 80: 681–687.

Burgess, S. C. et al. 2015. When is dispersal for dispersal? Unifying marine and terrestrial perspectives. - Biol. Rev., in press

Burton, O. J. et al. 2010. Trade-offs and the evolution of life-histories during range expansion. - Ecol. Lett. 13:

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

1210–1220.

Calcagno, V. et al. 2006. Coexistence in a metacommunity: The competition-colonization trade-off is not dead. - Ecol. Lett. 9: 897–907.

Caswell, H. 1990. Matrix Population Models. - Biometrics 46: 1238.

Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. - Ecol. Lett. 12: 197–209.

Clutton-Brock, T. and Sheldon, B. C. 2010. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. - Trends Ecol. Evol. 25: 562–573.

Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. - Annu. Rev. Ecol. Syst. 29: 141–177.

Cote, J. and Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. - Proc. Biol. Sci. 274: 383–390.

Cote, J. et al. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. - Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365: 4065–4076.

Cote, J. et al. 2013. Personality-dependent dispersal cancelled under predation risk. - Proc. R. Soc. B Biol. Sci. 280: 20132349.

Cotto, O. et al. 2014. Optimal Life-History Strategy Differs between Philopatric and Dispersing Individuals in a Metapopulation. - Am. Nat. 183: 384–393.

Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. - Oikos 121: 1337–1350.

De Meester, N. and Bonte, D. 2010. Information use and density-dependent emigration in an agrobiont spider. - Behav. Ecol. 21: 992–998.

De Meester, L. et al. 2016. Evolving Perspectives on Monopolization and Priority Effects. - Trends Ecol. Evol. 31: 136–146.

Debeffe, L. et al. 2014. Parasite abundance contributes to condition-dependent dispersal in a wild population of large herbivore. – Oikos 123: 1121-1125.

Duckworth, R. a and Badyaev, A. V 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. - Proc. Natl. Acad. Sci. U. S. A. 104: 15017–15022.

Duplouy, A. et al. 2013. Life history of the Glanville fritillary butterfly in fragmented versus continuous landscapes. - Ecol. Evol. 3: 5141–5156.

Dytham, C. and Travis, J. 2006. Evolving dispersal and age at death. - Oikos 113: 530–538.

Edelaar, P. et al. 2008. Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. - Evolution (N. Y). 62: 2462–2472.

Ellers, J. et al. 2011. Genotypic richness and phenotypic dissimilarity enhance population performance. - Ecology 92: 1605–1615.

Ezard, T. H. G. et al. 2009. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. - Philos. Trans. R. Soc. B Biol. Sci. 364: 1491–1498.

Fountain, T. et al. 2016. Predictable allele frequency changes due to habitat fragmentation in the Glanville fritillary butterfly. - Proc. Natl. Acad. Sci. U. S. A. 113: 2678–83.

Fronhofer, E. A. and Altermatt, F. 2015. Eco-evolutionary feedbacks during experimental range expansions. - Nat. Commun. 6: 6844.

Gaillard, J.-M. et al. 1989. An analysis of demographic tactics in birds and mammals. - Oikos 56: 59–76.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Goodacre, S. L. et al. 2009. Microbial modification of host long-distance dispersal capacity. - BMC Biol. 7: 32.

Gu, H. and Danthanarayana, W. 1992. Quantitative genetic analysis of dispersal in Epiphyas postvittana. II. Genetic covariations between flight capacity and life-history traits. - Heredity (Edinb). 68: 61–69.

Guerra, P. A. 2011. Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. - Biol. Rev. 86: 813–835.

Gyllenberg, M. et al. 2011. Body condition dependent dispersal in a heterogeneous environment. - Theor. Popul. Biol. 79: 139–54.

Hanski, I. and Saccheri, I. 2006. Molecular-level variation affects population growth in a butterfly metapopulation. - PLoS Biol. 4: 719–726.

Hanski, I. and Mononen, T. 2011. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. - Ecol. Lett. 14: 1025–34.

Higgins, S. I. et al. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? - Ecology 84: 1945–1956.

Hillaert, J. et al. 2015. The evolution of thermal performance can constrain dispersal during range shifting. - J. Biol. Dyn. 9: 317–335.

Holt, R. D. 2009. Darwin, Malthus, and movement: a hidden assumption in the demographic foundations of evolution. - Isr. J. Ecol. Evol. 55: 189–198.

Huang, F. et al. 2015. Rapid evolution of dispersal-related traits during range expansion of an invasive vine Mikania micrantha. - Oikos 124: 1023–1030.

Jacob, S. et al. 2015. Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. - Evol. Ecol. 29: 851–871.

Jeschke, J. M. and Strayer, D. L. 2008. Are threat status and invasion success two sides of the same coin? - Ecography (Cop.). 31: 124–130.

Kisdi, E. et al. 2013. Evolution of condition-dependent dispersal - Oxford Scholarship. - In: Clobert, J. et al. (eds), Dispersal Ecology and Evolution. Oxford University Press, pp. 131–151.

Klemme, I. and Hanski, I. 2009. Heritability of and strong single gene (Pgi) effects on life-history traits in the Glanville fritillary butterfly. - J. Evol. Biol. 22: 1944–1953.

Korsten, P. et al. 2013. Genetic integration of local dispersal and exploratory behaviour in a wild bird. - Nat. Commun. 4: 2362.

Kubisch, A. et al. 2014. Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. - Oikos 123: 5–22.

Leibold, M. A. et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. - Ecol. Lett. 7: 601–613.

Li, J. and Margolies, D. C. 1994. Responses to direct and indirect selection on aerial dispersal behaviour in Tetranychus urticae. - Heredity (Edinb). 72: 10–22.

Lindström, J. 1999. Early development and fitness in birds and mammals. - Trends Ecol. Evol. 14: 343–348.

Lortie, C. J. et al. 2004. Rethinking plant community theory. - Oikos 107: 433–438.

Marshall, D. J. et al. 2010. Phenotype-environment mismatches reduce connectivity in the sea. - Ecol. Lett. 13: 128–140.

Merow, C. et al. 2014. Advancing population ecology with integral projection models: A practical guide. - Methods Ecol. Evol. 5: 99–110.

Miner, B. G. et al. 2005. Ecological consequences of phenotypic plasticity. - Trends Ecol. Evol. 20: 685–692.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Negoita, L. et al. 2015. Isolation-driven functional assembly of plant communities on islands. – Ecography, in press

Niitepõld, K. 2010. Genotype by temperature interactions in the metabolic rate of the Glanville fritillary butterfly. - J. Exp. Biol. 213: 1042–1048.

Niitepõld, K. et al. 2009. Flight metabolic rate and Pgi genotype influence butterfly dispersal rate in the field. - Ecology 90: 2223–2232.

Ozgul, A. et al. 2010. Coupled dynamics of body mass and population growth in response to environmental change. - Nature 466: 482–485.

Phillips, B. L. 2015. Evolutionary processes make invasion speed difficult to predict. - Biol. Invasions 17: 1949–1960.

Phillips, B. L. et al. 2010. Life-history evolution in range-shifting populations. - Ecology 91: 1617–1627.

Pinto, S. M. et al. 2014. Seed dispersal is more limiting to native grassland diversity than competition or seed predation. - J. Ecol. 102: 1258–1265.

Réale, D. et al. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. - Philos. Trans. R. Soc. Lond. B. Biol. Sci. 365: 4051–4063.

Roff, D. A. 1994. Evidence That the Magnitude of the Trade-Off in a Dichotomous Trait is Frequency Dependent. - Evolution (N. Y). 48: 1650-1656.

Roff, D. A. and Bradford, M. J. 1996. Quantitative genetics of the trade-off between fecundity and wing dimorphism in the cricket Allonemobius socius. - Heredity (Edinb). 76: 178–185.

Roff, D. A. and Fairbarn, D. J. 2011. Path analysis of the genetic integration of traits in the sand cricket: a novel use of BLUPs. - J. Evol. Biol. 24: 1857–1869.

Ronce, O. 2007. How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution. - Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Ronce, O. et al. 2000. Landscape dynamics and evolution of colonizer syndromes: interactions between reproductive effortand dispersal in a metapopulation. - Evol. Ecol. 14: 233–260.

Ronce, O. et al. 2012. Dispersal syndromes. - In: Clobert, J. et al. (eds), Dispersal ecology and evolution. Oxford University Press, pp. 119–138.

Salguero-Gómez, R. et al. 2016. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. - Proc. Natl. Acad. Sci. U. S. A. 113: 230–235.

Selwood, K. E. et al. 2015. The effects of climate change and land-use change on demographic rates and population viability. - Biol. Rev. 90: 837–853.

Shima, J. S. et al. 2015. Consequences of variable larval dispersal pathways and resulting phenotypic mixtures to the dynamics of marine metapopulations. - Biol. Lett. 11: 20140778.

Shine, R. et al. 2011. An evolutionary process that assembles phenotypes through space rather than through time. - Proc. Natl. Acad. Sci. U. S. A. 108: 5708–5711.

Smallegange, I. M. and Coulson, T. 2013. Towards a general, population-level understanding of eco-evolutionary change. - Trends Ecol. Evol. 28: 143–148.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies. - J. Anim. Ecol. 46: 337–365.

Stearns, S. C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. - Oikos 41: 173–187.

Stearns, S. C. S. 1989. Trade-Offs in Life-History Evolution. - Functional 3: 259–268.

Stevens, V. M. et al. 2010. A meta-analysis of dispersal in butterflies. - Biol. Rev. Camb. Philos. Soc. 85: 625–

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

642.

Stevens, V. M. et al. 2013. Dispersal syndromes and the use of life-histories to predict dispersal. - Evol. Appl. 6: 630–642.

Stevens, V. M. et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. 17: 1039–1052.

Tarwater, C. E. and Beissinger, S. R. 2012. Dispersal polymorphisms from natal phenotype-environment interactions have carry-over effects on lifetime reproductive success of a tropical parrot (J-M Gaillard, Ed.). - Ecol. Lett. 15: 1218–1229.

terHorst, C. P. et al. 2010. Evolution of prey in ecological time reduces the effect size of predators in experimental microcosms. - Ecology 91: 629–636.

Therry, L. et al. 2014a. Integrating large-scale geographic patterns in flight morphology, flight characteristics and sexual selection in a range-expanding damselfly. 37: 1012–1021.

Therry, L. et al. 2014b. What factors shape female phenotypes of a poleward-moving damselfly at the edge of its range? 112: 556–568.

Thompson, K. et al. 2002. Seed dispersal: the search for trade-offs. - Dispersal Ecol. 42nd Symp. Br. Ecol. Soc.: 152.

Thomson, F. J. et al. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. - J. Ecol. 99: 1299–1307.

Travis, J. M. J. et al. 2012. Modelling dispersal: An eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. - Methods Ecol. Evol. 3: 628–641.

Urban, M. C. and De Meester, L. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. - Proc. Biol. Sci. 276: 4129–4138.

Van Allen, B. G. and Bhavsar, P. 2014. Natal habitat effects drive density-dependent scaling of dispersal decisions. - Oikos 123: 699–704.

Van Dyck, H. and Baguette, M. 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? - Basic Appl. Ecol. 6: 535–545.

Van Petegem, K. et al. 2015. Empirically simulated spatial sorting points at fast epigenetic changes in dispersal behaviour. - Evol. Ecol. 29: 299-310.

Van Petegem, K. et al. 2016. Spatial selection and local adaptation jointly shape life-history evolution during range expansion. - Am. Nat., in press

Vellend, M. 2010. Conceptual synthesis in community ecology. - Q. Rev. Biol. 85: 183–206.

Vellend, M. et al. 2014a. Drawing ecological inferences from coincident patterns of population- and community-level biodiversity. - Mol. Ecol. 23: 2890–2901.

Vellend, M. et al. 2014b. Assessing the relative importance of neutral stochasticity in ecological communities. - Oikos 123: 1420–1430.

Vindenes, Y. and Langangen, Ø. 2015. Individual heterogeneity in life histories and eco-evolutionary dynamics. - Ecol. Lett. 18: 417–432.

Weigang, H. C. and Kisdi, É. 2015. Evolution of dispersal under a fecundity-dispersal trade-off. - J. Theor. Biol. 371: 145–153.

Williams, J. L. et al. 2016. The Influence of Evolution on Population Spread through Patchy Landscapes (BM Bolker and AA Winn, Eds.). - Am. Nat., in press

Yan, H. et al. 2014. Eusocial insects as emerging models for behavioural epigenetics. - Nat. Rev. Genet. 15: 677–88.

bioRxiv preprint doi: https://doi.org/10.1101/065151; this version posted July 21, 2016. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Yu, D. W. and Wilson, H. B. 2001. The Competition-Colonization Trade-off Is Dead ; Long Live the Competition-Colonization Trade-off. - Am. Nat. 158: 49–63.

Zera, A. J. and Brisson, J. A. 2012. NoQuantitative, physiological, and molecular genetics of dispersal/migration. - In: Clobert, J. et al. (eds), Dispersal: Causes and Consequences. Oxford University Press, pp. 63–82.