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REVIEW AND SYNTHESIS

Life-history syndromes: Integrating dispersal through space and time

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Abstract

Recent research has highlighted interdependencies between dispersal and other life-history traits, i.e. dispersal syndromes, thereby revealing constraints on the evolution of dispersal and opportunities for improved ability to predict dispersal by considering suites of dispersal-related traits. This review adds to the growing list of life-history traits linked to spatial dispersal by emphasising the interdependence between dispersal through space and time, i.e. life-history diversity that distributes individuals into separate reproductive events. We reviewed the literature that has *simultaneously* investigated spatial and temporal dispersal to examine the prediction that traits of these two dispersal strategies are negatively correlated. Our results suggest that negative covariation is widely anticipated from theory. Empirical studies often reported evidence of weak negative covariation, although more complicated patterns were also evident, including across levels of biological organisation. Existing literature has largely focused on plants with dormancy capability, one or two phases of the dispersal process (emigration and/or transfer) and a single level of biological organisation (theory: individual; empirical: species). We highlight patterns of covariation across levels of organisation and conclude with a discussion of the consequences of dispersal through space and time and future research areas that should improve our understanding of dispersal-related life-history syndromes.

Keywords

Dispersal syndromes, dispersal traits, eco-evolutionary dynamics, risk spreading, spatial dispersal, stochastic environments, temporal dispersal, trait-based approach.

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> "*As usually understood, dispersal implies movement in space… But dispersal can as well be viewed as movement in time, for instance by dormant seeds. We believe it is appropriate to consider the temporal and spatial dimensions of dispersal jointly, especially in the context of life history evolution….*" (Eriksson & Kiviniemi 1999)

> "*Organisms can succeed in unstable environments by dispersing to favourable habitats randomly, or in a directed fashion. As has been long recognised, dispersal may be either temporal or spatial; therefore, diapause and migration can be thought of as alternative strategies for spreading risk through time and space.*" (Bohonak & Jenkins 2003)

INTRODUCTION

Dispersal, or the suite of behaviours that results in the movement of individuals away from their natal population to a different breeding population, is ubiquitous in nature and remains a central topic in ecology and evolution (Ronce 2007; Clobert *et al*. 2012). Dispersal serves multiple functions, such as avoiding harsh conditions, reducing kin competition or spreading risk among offspring, and has consequences for gene flow (reviewed in Matthysen 2012; Duputié & Massol 2013). Dispersal is a multi-stage process, and can be decomposed into its component stages of emigration, transfer and settlement, each with associated costs and risks that influence the performance of dispersers (Bonte *et al*. 2012; Travis *et al*. 2012). As examples, dispersal carries costs associated with the development of morphological structures necessary to disperse (e.g. wings), risk of mortality incurred during the transfer stage and risk that dispersing individuals will arrive in an unfavourable environment (reviewed in Bonte *et al*. 2012). Moreover, costs during one phase can trade-off and feedback to influence costs at another phase (Bonte *et al*. 2012; Travis *et al*. 2012). Because selection will act to maximise fitness by minimising overall dispersal costs, trade-offs will result in suites of co-adapted traits that influence dispersal. These trade-offs are likely to influence other traits that may be linked with dispersal, thereby inducing *dispersal syndromes* (i.e. patterns of covariation among phenotypic traits associated with dispersal, Ronce & Clobert 2012).

The burgeoning literature on dispersal syndromes has identified numerous examples of morphological, behavioural and life-history traits that correlate with dispersal (reviewed in Ronce & Clobert 2012). Recent work by Stevens *et al*. (2012, 2013) highlighted the interdependency of dispersal and other life-history traits. Using butterflies as a model system, these researchers reviewed the evidence for correlations (both positive and negative) between dispersal and a suite of life-history traits, including traits associated with demography, morphology, ecological specialisation and behaviours involved in movement (Stevens *et al.* 2012). Their results revealed that butterfly life histories were strongly associated with their dispersal ability (Stevens *et al.* 2013), and they presented a compelling argument that investigating these *life-history syndromes* holds considerable promise for improving our ability to predict dispersal (see also Whitmee & Orme 2013). In general, investigating the relationship between dispersal and other life-history traits has clear relevance for understanding the evolution of dispersal (Ronce & Clobert 2012), adaption to environmental change (Travis *et al.* 2013) and invasion success (Perkins *et al.* 2013).

Here, we investigate how spatial dispersal integrates with life-history traits that distribute individuals into separate reproductive events, i.e. temporal dispersal (see Cohen 1966; Bakshtansky 1980; Bohonak & Jenkins 2003; Duputié & Massol 2013). Both spatial and temporal dispersal can be viewed as risk-spreading strategies for persisting through stochastic and changing conditions (Levin *et al.* 1984; McPeek & Kalisz 1998; Bohonak & Jenkins 2003; Siewert & Tielbörger 2010; Gremer & Venable 2014). For example, risk of reproductive failure can be dispersed within years (e.g. through variation in timing of breeding or through multiple clutches) or among years (e.g. through variation in age at maturity or iteroparity). That both types of dispersal traits can reduce the risk of reproductive failure suggests that they might substitute for one another. More generally, this implies that dispersal through space might constrain the evolution of dispersal through time, and vice versa.

Although the idea that spatial and temporal dispersal are alternative risk spreading strategies was introduced almost half a century ago by Den Boer (1968), this possibility has not garnered much attention in the burgeoning literature on dispersal syndromes. Moreover, most research continues to focus on risk spreading through either spatial (e.g. Clobert *et al.* 2001, 2012; Kisdi 2002; Ronce 2007 for review) or temporal (e.g. Menu *et al.* 2000; Gourbière & Menu 2009) dispersal, with far less attention on *risk spreading through combinations of these strategies* (Fig. 1c). This is unfortunate because understanding the evolution of risk spreading through dispersal requires understanding the covariation between these dispersal strategies (e.g. McPeek & Kalisz 1998; Eriksson & Kiviniemi 1999; Vitalis *et al.* 2013).

The overall goal of this study is to review studies that have *simultaneously* investigated dispersal through space and time to examine the assumption that the two are negatively correlated (Bohonak & Jenkins 2003; Vitalis *et al.* 2013). We begin by highlighting recent advances from the study of spatial dispersal that might be profitably applied to the study of temporal dispersal, and then we synthesise results from theoretical and empirical studies exploring correlations between traits of the two dispersal strategies. Researchers have studied dispersal traits at different levels of biological organisation, so we also highlight patterns across levels of organisation and introduce a framework for studying dispersal patterns across multiple organisational levels. We then discuss the population-level consequences of dispersal through space and time and the conservation and management implications of recognising that organisms might spread risk in different ways. Finally, we discuss future research areas that should improve our understanding of the joint evolution of dispersal through space and time.

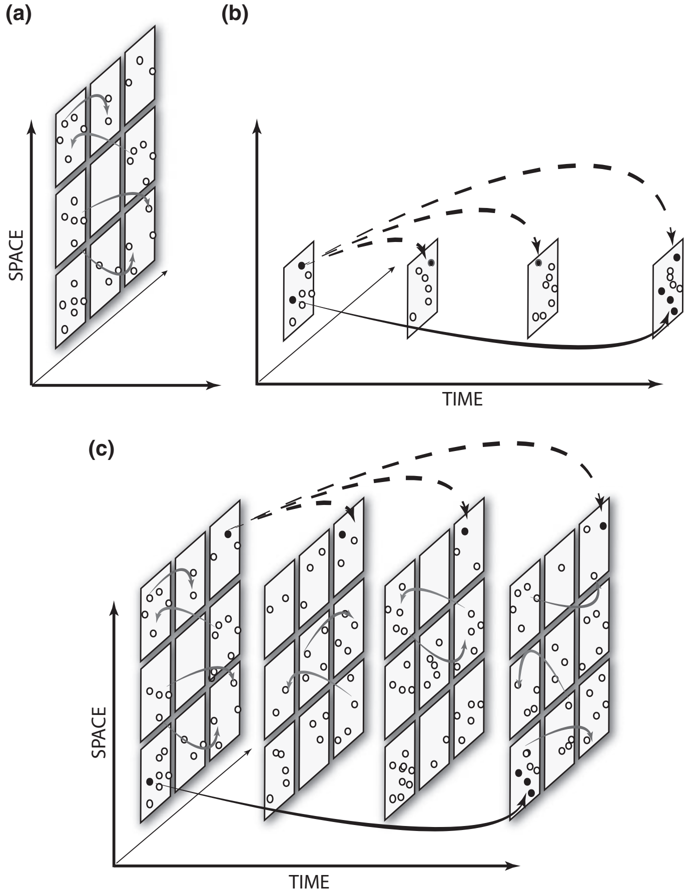

Figure 1 A conceptual diagram emphasising dispersal through space and/or time. Panel (a) represents spatial dispersal within a generation (solid grey arrows). Panel (b) represents temporal dispersal (between generations). Temporal dispersal can be achieved through, e.g. age structure and iteroparity (dashed black arrows) or diapause or dormancy (solid black arrow). Panel (c) represents combinations of dispersal through space and time.

ADVANCES AND INSIGHTS FROM SPATIAL DISPERSAL ARE RELEVANT TO THE STUDY OF TEMPORAL DISPERSAL

One of our aims in this paper is to advance the idea that dispersal through time should be integrated into studies of dispersal-related life-history syndromes. Such integration will improve our understanding of the constraints on dispersal traits as well as the consequences of dispersal syndromes for population dynamics. As part of this effort, it is useful to ask: can insights and methodological advances from the study of spatial dispersal be used to advance the study of temporal dispersal and associated life-history syndromes? For example, one recent emphasis within the spatial dispersal literature has been on the explicit consideration of three phases of dispersal: emigration, transfer or movement, and settlement (Travis *et al.* 2012). We argue that direct analogues exist for temporal dispersal: emigration (e.g. entering dormancy), transfer (e.g. surviving through dormancy) and settlement (e.g. emerging from dormancy).

Consequently, through our literature review, we highlight the stage of dispersal considered in studies when specified.

Another recent emphasis within the spatial dispersal literature has been on informed dispersal, meaning dispersal decisions that are affected by cues or information (e.g. environmental or physiological cues, density of conspecifics or public information; Clobert *et al.* 2009). Indeed, different sources of internal and external information can be used to guide spatial dispersal decisions at all stages of the dispersal process (Bowler & Benton 2009; Chaput-Bardy *et al.* 2010; Clobert *et al.* 2012). It seems likely that similar sources of internal and external information might also be used to guide temporal dispersal decisions. For example, organisms might use external cues such as temperature to determine when to emerge from dormancy to take advantage of peak resource availability or avoid predation (e.g. Hairston *et al.* 1990; Khatchikian *et al.* 2010; Snodgrass *et al.* 2012). The quality of information (e.g. reliability of cues) may also influence how context-dependent dispersal strategies evolve. For example, different levels of information, its accuracy and the cost of acquiring information all have consequences for the evolution of spatial dispersal (Enfjäll & Leimar 2009; Bocedi *et al.* 2012). It seems likely that the quality of information might also have consequences for the evolution of temporal dispersal, and for the joint evolution of dispersal through space and time.

The study of spatial dispersal has also benefited from methodological advances, including developments in the field of genetics that have led to a renewed interest in measuring dispersal and tracking dispersers (e.g. Rieux *et al.* 2013; see Tesson & Edelaar 2013 for review). New methods are sensitive enough to quantify effective dispersal among populations, opening the door to studies of ‘effective’ temporal dispersal, i.e. understanding the contribution of cohorts to buffering populations (e.g. López-Sepulcre *et al.* 2013).

While the above examples all serve to highlight the potential gains of applying the concepts and methods developed for the study of spatial dispersal to the study of temporal dispersal, not all advances have direct analogues. For example, there has been growing interest in the ecological and evolutionary consequences of long-distance dispersal events (e.g. Bohrer *et al.* 2005; Nathan 2006). For example, seeds might be further dispersed by large herbivores beyond the dispersal distance assumed based on morphological adaptations for dispersal. In this case, it is not clear that there is a temporal analogue to long-distance dispersal events, although prolonged diapause may favour recolonisation, invasion and resistance over shorter diapause (Mahdjoub & Menu 2008; Solbreck & Widenfalk 2012). Consequently, for this review, we will use the term ‘spatial dispersal’ to refer to ‘common’ spatial dispersal events that occur within the expected morphological or physiological abilities of the study organisms, and not to extreme or rare long-distance dispersal events.

COVARIATION OF DISPERSAL THROUGH SPACE AND TIME: INSIGHTS FROM THEORETICAL STUDIES

To examine the assumption of negative covariation between dispersal through space and time, we reviewed the literature examining the joint patterns of dispersal. We first searched Web of Science for pertinent articles (published before 2014) using the following terms: ‘risk-spreading’, ‘bet-hedging’ or ‘dispersal’ in combination with other terms such as ‘temporal’, ‘dormancy’, ‘diapause’, ‘delayed germination’, ‘overlapping generations’ or ‘age-structure’. For the subset of relevant articles, we then reviewed the references cited section of each article to identify earlier work on the topic, and performed a forward search on Web of Science to identify recent articles exploring these same themes.

We found 25 theoretical studies that simultaneously explored dispersal through space and time (Appendix S1). These studies employed diverse approaches for quantifying patterns of covariation between dispersal traits, tended to focus more on dispersal rate and less on dispersal distance and typically focused on just a single phase of the dispersal process – emigration (but see Eriksson 2000; Laterra & Solbrig 2001; Vitalis *et al.* 2013) (Appendix S1). The vast majority of studies using analytical or simulation approaches (12 of 14) reported evidence of a trade-off between the two dispersal strategies in uncertain environments (Appendix S1). Moreover, these studies reported that (1) spatial and temporal dispersal are alternative strategies that can evolve in response to environmental variability and (2) selection for one dispersal trait reduces selection for the other. Two other studies assumed a trade-off between dispersal through space and time and instead explored the conditions under which more complicated patterns emerged (Snyder 2006; Vitalis *et al.* 2013).

Conditions favouring dispersal in space and/or time

Several theoretical studies explored the conditions under which spatial dispersal is favoured over temporal dispersal and vice versa. Overall, these studies have found that *spatial dispersal is favoured over temporal dispersal* when (1) the environment is only occasionally favourable, (2) the number of suitable habitats increases, (3) the cost of spatial dispersal is low relative to the cost of temporal dispersal, (4) conditions differ among sites but are similar among years and (5) when meta-populations are young and populations are characterised by fast growth (see Levin *et al.* 1984; Cohen & Levin 1991; Wiener & Tuljapurkar 1994; McPeek & Kalisz 1998; Olivieri 2001).

In contrast, *temporal dispersal is favoured over spatial dispersal* (1) in small meta-populations, (2), when fitness failures are likely to occur simultaneously in all patches of a meta-population, (3) when the cost of spatial dispersal is high relative to the cost of temporal dispersal, (4) when conditions differ among years but are similar among sites and (5) in an older meta-population with low population growth (see Cohen & Levin 1991; Olivieri *et al.* 1995; Olivieri & Gouyon 1997; McPeek & Kalisz 1998; Eriksson & Kiviniemi 1999).

Autocorrelation in environmental conditions can influence patterns of covariation

The theoretical studies we identified also highlighted the degree of autocorrelation in environmental conditions as a factor influencing patterns of trait covariation (Levin *et al.* 1984; Snyder 2006) (Fig. 2). Positive spatial or temporal autocorrelation in the environment suggests that conditions in the current site or temporal period (e.g. days, weeks, years or decades, depending on the life span of the organism considered) resemble conditions in a nearby site or the previous period, whereas negative temporal or spatial autocorrelation indicates the opposite. No temporal or spatial autocorrelation implies that the environment fluctuates randomly through space or time. Only one of the cases we discussed in the previous section explicitly addressed autocorrelation in the environment (point d, Fig. 2). However, theory indicates that both dispersal strategies are *favoured* when environmental conditions are variable in space and time (i.e. when both spatial and temporal autocorrelation in environmental conditions are negative or weak, Fig. 2), but are *selected against* when environmental conditions are similar from one year to the next and from site to site (i.e. when spatial and temporal autocorrelation in environmental conditions are both positive, Fig. 2) (Venable & Brown 1988; Cohen & Levin 1991; Wiener & Tuljapurkar 1994).

COVARIATION OF DISPERSAL THROUGH SPACE AND TIME: INSIGHTS FROM EMPIRICAL STUDIES

While theory and models suggest that negative covariation between dispersal in space and time can evolve readily and that more complicated patterns can evolve under different environmental conditions (Fig. 2), are the two negatively correlated *in nature*? To address this question, we reviewed empirical studies that simultaneously considered dispersal through space and time (using the same approach as with the theoretical studies). We found 18 empirical studies (Appendix S2), nearly all of which focused on plants with dormancy capability. The patterns from these studies were less uniform than those from theoretical studies. Several empirical studies reported evidence of significant (Shapovalov & Taft 1954; Venable & Lawlor 1980; McEvoy 1984; Venable *et al.* 1985; Rees 1993; Imbert 1999; Bégin & Roff 2002; Westley *et al.* 2013) or weak (Eriksson 1996; Bégin & Roff 2002; Dostál 2005; Pélisson *et al.* 2013) negative covariation, whereas others report more complicated patterns (Willson *et al.* 1993; Siewert & Tielbörger 2010) or no relationship at all (Eriksson 1992; Stevens *et al.* 2013) (Appendix S2).

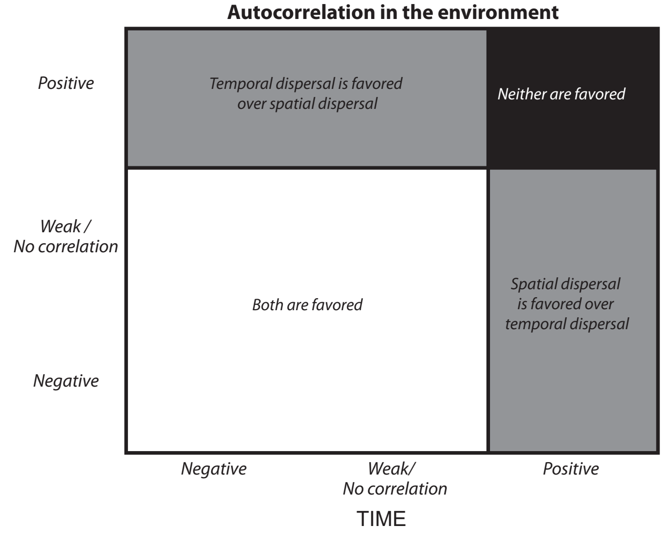

Figure 2 A space–time dispersal matrix highlighting how autocorrelation in environmental conditions influences patterns of covariation between dispersal through space and time.

Within the empirical studies, there was a better balance between studies that focused on dispersal capacity or rate as a measure of dispersal (nine studies) and/or studies that considered dispersal distance (nine studies). The majority of empirical studies focused on the *emigration* stage of dispersal for both dispersal traits (14 studies), while a handful also estimated survival during the *transfer* stage (8 studies), and only two studies investigated the *settlement* stage (Appendix S2).

Eleven of the 18 empirical studies focused on plants, including four that focused exclusively on seed dimorphism (i.e. 'migrant' vs. 'dormant' seeds), which is thought to reflect an adaptation to unpredictable environmental conditions (Venable & Lawlor 1980; McEvoy 1984; Venable & Levin 1985; Imbert 1999). These studies highlighted a potential mechanism explaining the observed negative covariation – the existence of a trade-off *within* seeds. Specifically, an individual seed that possessed attributes that facilitated spatial dispersal did not also possess attributes that facilitated temporal dispersal. Venable & Lawlor (1980) compiled a list of desert plants characterised by seed dimorphism and found a strong tendency for seeds to exhibit either low spatial dispersal ability and delayed germination (i.e. high temporal dispersal), or high spatial dispersal ability and quick germination (i.e. low temporal dispersal). Indeed, only 3 of the 28 species studied by Venable & Lawlor (1980) were characterised as having both high spatial and temporal dispersal capabilities. Negative covariation was also reported for two species with seed dimorphism in other regions (McEvoy 1984; Imbert 1999).

Beyond plants, dispersal through space and time has also been explored in invertebrates with diapause capability (Bégin & Roff 2002; Frisch 2002; Robinet *et al.* 2008; Pélisson *et al.* 2013; Stevens *et al.* 2013; Appendix S2). For example, Bégin & Roff (2002) investigated the occurrence of wing dimorphism (short vs. long wings) and diapause within a cricket population (*Gryllus veletis*) under laboratory and field conditions. In both settings, a high percentage of short-winged individuals (90%) and a low percentage of long-winged individuals (22%) experienced diapause, providing evidence of negative covariation between dispersal traits. In contrast, Pélisson *et al.* (2013) explored the spatial (flight performance) and temporal (variability in diapause duration within cohorts) dispersal capabilities of four co-occurring weevil species (*Curculio* spp.). Although these authors found evidence of a dispersal trade-off in two weevil species, they found no evidence of a trade-off in the other two species.

Although Den Boer (1968) argued that the spreading of risk in space and time should be common, few empirical examples have focused on the two dispersal strategies in vertebrates. This may be due to the difficulty of monitoring individuals and populations in both space and time across various environments or measuring dispersal (see Future directions). One exception comes from studies of dispersal strategies in Pacific salmon and trout (*Oncorhynchus* spp.). Bakshtansky (1980) and Quinn (1984) both emphasised that age complexity and iteroparity among salmonid fishes are forms of ‘protection in time’, whereas spatial dispersal between populations is a form of ‘protection in space’, suggesting a possible trade-off between the two strategies. For example, semelparous coho salmon (*O. kisutch*) dispersed to a non-natal site (‘protection in space’) at a higher rate than iteroparous steelhead trout (*O. mykiss*) (Shapovalov & Taft 1954). Similarly, Westley *et al.* (2013) reported that semelparous chinook salmon (*O. tshawytscha*) dispersed at a higher rate than iteroparous steelhead trout.

INTEGRATING ACROSS LEVELS OF ORGANISATION

Our review of empirical research exploring dispersal through space and time revealed that researchers have studied the two dispersal strategies at multiple levels of biological organisation (see Appendix S2), including at the individual, population and species level. This result prompted us to consider how expected and observed dispersal syndromes varied across levels of biological organisation (Fig. 3), with the initial expectation that patterns at one level would not scale up to higher levels (see also Ronce & Clobert 2012).

Theoretical insights

At the *individual level*, theory suggests we should observe negative covariation between dispersal in space and time due to mechanistic constraints (e.g. physiological trade-offs; Fig. 3a). For example, morphological structures that facilitate dispersal through space and time might compete for the same limited resources, leading to a physiological trade-off (e.g. flight capability and diapause in insects: Zera & Denno 1997).

This pattern of negative covariation within individuals could be masked at the *population level*, however, due to variation in the environment. This implies that patterns of covariation might differ among populations distributed in space (e.g. compare hypothetical populations 1–3 in Fig. 3b). For example, positive phenotypic correlation between traits could emerge at the population level even if an underlying (physiological) negative trade-offs exists, provided there is significant variation in acquisition and allocation of resources across a population. Van Noordwijk & De Jong (1986) proposed the ‘Y model’ in which two traits compete for the same resource at the individual level, but individuals differ both in their ability to acquire a resource and in their allocation of that resource to different traits. Individuals in a local environment with nearly unlimited resources or with a higher ability to acquire resources can allocate their energy to both traits, thus obscuring the underlying trade-off. Beyond resource availability and acquisition, variation in personality traits (Cote *et al.* 2010) or differential selection on dispersers and non-dispersers might also influence the patterns of trait covariation at the population level (Ronce & Clobert 2012).

As resource availability and selection pressures are likely to vary among populations in nature, this should lead to different patterns of trait covariation between the two dispersal strategies. However, we posit that some patterns of covariation are less likely to occur. For example, populations with low dispersal both in space and time would be highly vulnerable to extinction in stochastic environments. Similarly, populations with high dispersal capability in both space and time are likely rare, as an organism should not be able to maximise all elements of its fitness simultaneously (i.e. the Darwinian Demon: Law 1979) due to both genetic and physiological constraints. However, we are aware of at least some organisms that do seem to be capable dispersers through both time and space (e.g. many marine fishes) and others that are poor dispersers through both time and space (e.g. weevils, Pélisson *et al.* 2013), implying that such combinations are not impossible, but perhaps are rare. Taken together, these results hint that negative covariation may emerge when comparing dispersal traits across populations (Fig. 3b).

At the *species level*, some theoretical studies suggest that the covariation between spatial and temporal dispersal should be negative when comparing related species in a wide range of environments, or when comparing unrelated species occurring in the same environment (Cohen & Levin 1987, 1991; McPeek & Kalisz 1998). Similarly, we might expect to observe negative covariation between the dispersal traits of different species within a given environment (Fig. 3c) because of the storage effect (sensu Chesson 2000), wherein the coexistence of multiple species is facilitated by dispersal through space and time as individual species respond differently to environmental variation. Thus, theoretical research reveals that a negative pattern of covariation can emerge at multiple levels of biological organisation (individual, population and species), at least under some circumstances, but for different reasons (Fig. 3, left panel).

Empirical insights

Earlier we highlighted evidence of an apparent trade-off between spatial and temporal dispersal traits at the *individual level* from several studies focused on plants characterised by seed dimorphism (e.g. Venable & Lawlor 1980; Imbert 1999). Outside of plants, we found just one other study focused at individual level. Bégin & Roff (2002) provided evidence of negative covariation between wing dimorphism (short vs. long wings) and diapause within a cricket population (*Gryllus veletis*) (Fig. 3d). However, in comparing laboratory vs. field conditions, the authors highlighted a potential effect of environmental harshness on the expression of these dispersal traits. Under laboratory conditions, only 6% of individuals developed short wings compared to >95% in the wild, implying that the trade-off was relaxed under benign laboratory conditions. The authors also investigated the genetic basis of the trade-off and reported a positive phenotypic and genetic correlation between direct development (i.e. no diapause) and predisposition for long wings (i.e. high capacity for dispersal through space), indicating a heritable basis to this trade-off.

At the *population level*, we found two studies that examined patterns of covariation between dispersal traits. Gravuer *et al.* (2003) investigated the dispersal capacities of 14 populations of northern blazing star (*Liatris scariosa*, Asteraceae) and found a significant trade-off between spatial dispersal capabilities and germination success among populations (Fig. 3e), although they cautioned that their measure of germination success might have been influenced by variation in seed dor-

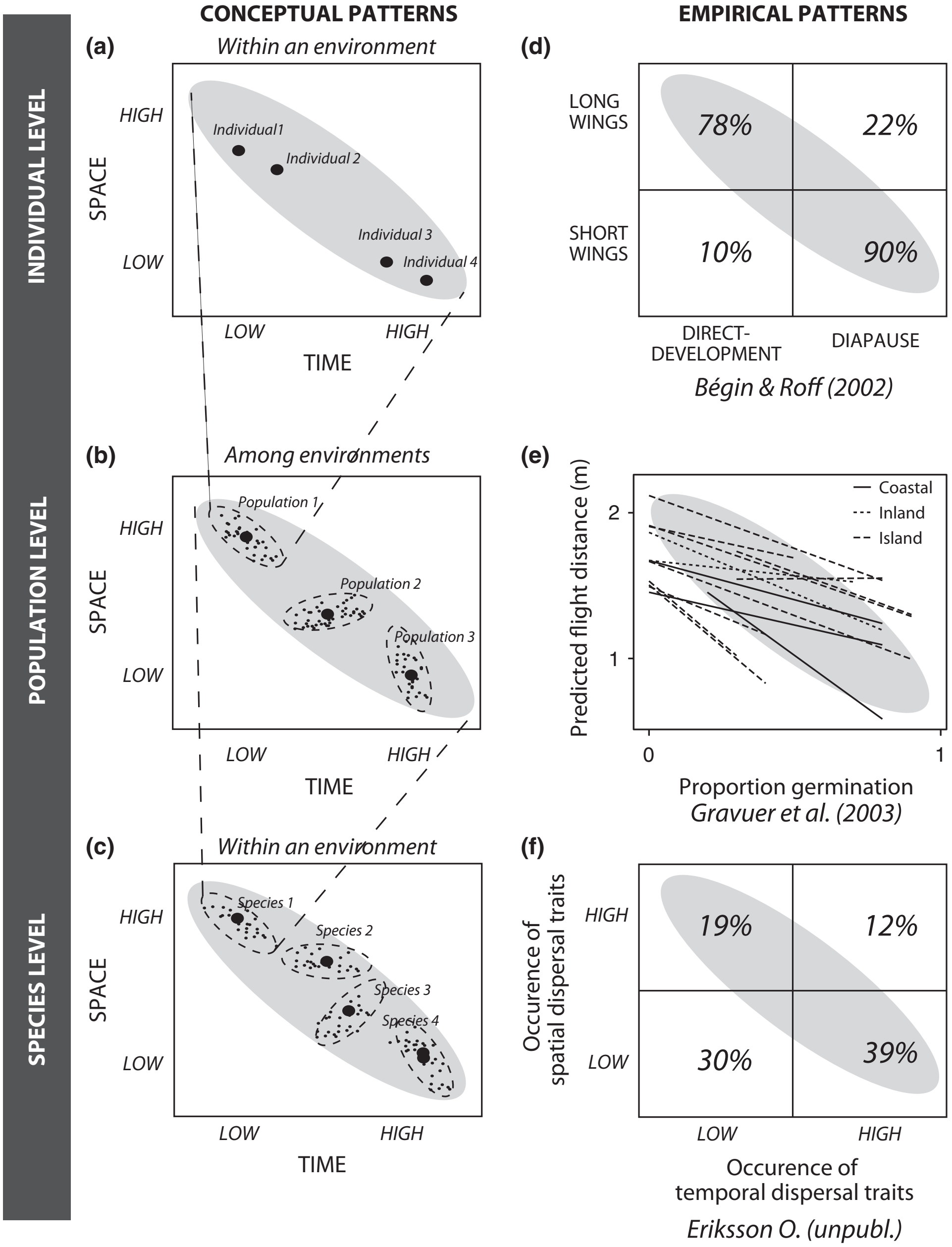

Figure 3 Covariation (grey ellipse) between dispersal through time (x-axis) and space (y-axis) at different levels of biological organisation: (a) individual, (b) population and (c) species. The left column includes conceptual diagrams to illustrate possible negative relationships. Depending on confounding factors (e.g. environmental conditions), we might expect various patterns of covariation within populations (b) and species (c), even if a trade-off exists at the individual level (a). The right column highlights empirical examples (see text for more details). For (d), Bégin & Roff (2002) reported that a high proportion of individuals experienced diapause among short-wings cricket (*Gryllus veletis*), but few long-wings individuals experienced diapause. For (e), Gravuer *et al.* (2003) reported negative covariation between spatial dispersal capacities (here, flight distance) and germination proportion among 14 populations of northern blazing star (*Liatris scariosa*). At the species level (f), Eriksson O. (unpubl. data) observed a weak trade-off among 98 plant species from Swedish grasslands.

mancy or intrinsic viability among different populations. Siewert & Tielbörger (2010) used an experimental approach to control spatial dispersal of 112 desert plant species, and then measured the consequences of that control in populations at five sites along a rainfall gradient. While there were no differences in trade-offs among populations, they found that patterns of trait covariation differed among species within sites, and included both positive and negative correlation coefficients (although negative coefficients were more common than positive ones).

Ten studies have examined patterns of covariation between spatial and temporal dispersal traits at the *species level* (summarised in Appendix S2). Rees (1993) synthesised data from long-term experimental studies on 171 species of British plants and found a highly significant reduction in seed dormancy in species that had efficient means of dispersing through space.

However, other multi-species comparison studies have reported conflicting results. Exploring the dispersal capabilities of 61 angiosperm species, Eriksson (1992) found no relationship between the occurrence of a seed bank (temporal dispersal) and ability of seeds to disperse in space. In a separate study, Eriksson (1996) found that the majority of species in Swedish semi-natural grasslands and deciduous forests displayed temporal dispersal capabilities, but lacked obvious traits that facilitated spatial dispersal (see also Fig. 3f). Similarly, Willson *et al.* (1993) explored dispersal trade-offs in 89 species of herbaceous plants and found that only a few species with poor mechanisms for dispersal through space had better temporal dispersal capabilities. Other studies have focused on the covariation between spatial dispersal traits and other life-history traits (i.e. dispersal syndromes) in various species of butterfly (Stevens *et al.* 2012, 2013; Baguette & Stevens 2013). While the objective of these studies was not to identify a trade-off between dispersal in space and time, diapause capability was included in their analysis of life-history traits. The authors did not find evidence of a correlation between temporal and spatial dispersal, although they highlighted that the binomial metric of temporal dispersal did not allow adequate exploration of this relationship (Stevens *et al.* 2012).

Overall, these findings imply that negative covariation between dispersal through space and time can be observed under some conditions, and at multiple levels organisation. However, most theoretical studies exploring patterns of covariation have focused on a similar level of organisation (individual level) and on a similar stage of the dispersal process (emigration) (Appendix S1). Empirical studies are similarly limited in scope – most have focused on plants with dormancy capability, at a similar level of organisation (species level) and on a similar stage of the dispersal process (emigration) (Appendix S2). Consequently, these results across levels should be interpreted cautiously. Ultimately, we expect that genetic and environmental sources of variation as well as natural selection will shape dispersal-related life history syndromes across levels of biological organisation. Teasing apart the relative influence of these factors in shaping dispersal patterns continues to be a major challenge in advancing a general theory of dispersal, but variation in dispersal syndromes can also be viewed as a *source* of information on the causes and consequences of the evolution of dispersal (Ronce & Clobert 2012).

ECO-EVOLUTIONARY DYNAMICS: CONSEQUENCES OF DISPERSAL THROUGH SPACE AND TIME FOR POPULATION DYNAMICS

> "*The chance of survival of a population may even be increased, because the variation within the population makes it possible to cope with the variation in space and time of the habitat. This possibility led me to formulate the concept 'spreading of risk*'". Den Boer (1968)

While our review has focused on elucidating patterns of covariation between dispersal through space and time, it is also important to consider the *consequences* of alternative dispersal strategies for population dynamics. Den Boer (1968) early research on the topic suggested that spreading risk in space and time are both mechanisms that stabilise population size and favour persistence (Fig. 4, see also Reddingius & Den Boer 1970). Next, we highlight research exploring the ecological consequences of dispersal through space and time.

Numerous theoretical studies have explored the consequences of either spatial or temporal dispersal on population persistence (e.g. Bowler & Benton 2005 for spatial dispersal; Menu *et al.* 2000 for temporal dispersal), in general doing so by quantifying the evolutionary stable strategy (Levin *et al.* 1984; Olivieri 2001; Snyder 2006; Vitalis *et al.* 2013) or the geometric growth rate (Wiener & Tuljapurkar 1994; McPeek & Kalisz 1998; Mathias *et al.* 2001). However, few studies have linked *dispersal syndromes* with population dynamics (Duputié & Massol 2013). McPeek & Kalisz (1998) and Eriksson (1996) proposed that temporal dispersal provides more long-term persistence capability than spatial dispersal, as populations characterised by temporal dispersal properties have 'population inertia' that delays extinction even when the population growth rate falls below unity. However, none of these studies have quantified the risk of extinction or the relative importance of dispersal syndromes for buffering populations. Schreiber (2010) makes a start on some of these directions by exploring the effects of temporal and spatial heterogeneity of the environment (including autocorrelation) on population persistence using a theoretical model, although his model does not explicitly consider temporal dispersal capacity.

We found no empirical studies exploring the relative importance of the two dispersal strategies for sustaining populations

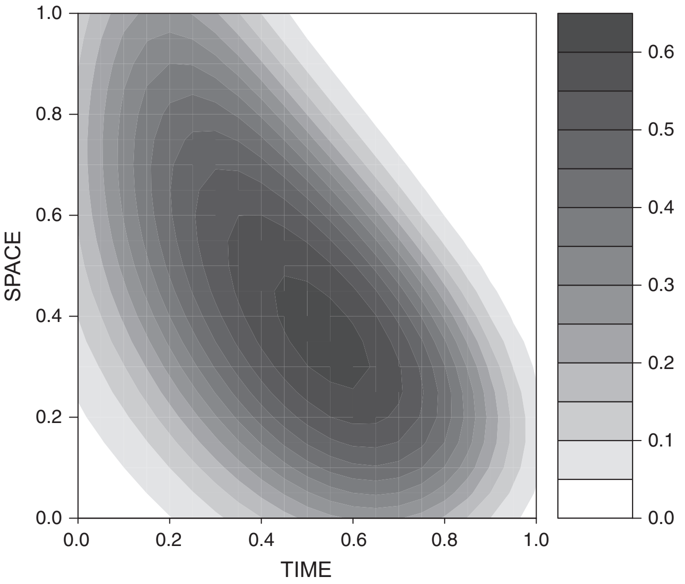

Figure 4 This diagram highlights a hypothesised relationship between persistence probabilities as a function of spatial and temporal dispersal strategies. This relationship was obtained from simulations using a positive effect of both dispersal strategies on persistence, but a negative effect of interactions between the two. This hypothesis is based on our expectations regarding the effects of constraints and natural selection, which should maximise the fitness of organisms spreading their risk along a continuum from high spatial dispersal/low temporal dispersal to low spatial dispersal/high temporal dispersal. This hypothesis remains to be tested and it is more likely that complex patterns will emerge and be context dependent.

in the wild. However, a handful of studies have quantified the relative contribution of alternative dispersal strategies to recruitment success. Dostál (2005) investigated the population turnover of five annual plant species in a temperate grassland ecosystem and estimated spatial dispersal and seed bank abundance (i.e. temporal dispersal) for species that colonised small habitat patches. While the author observed extensive seed banks, he also found that the seed bank played a minor role in recruitment dynamics compared to spatial dispersal, possibly due to low environmental stochasticity. In contrast, Siewert & Tielbörger (2010) reported only a weak contribution of spatial dispersal to seedling recruitment in desert plants, leading these authors to conclude that dormancy might be a superior strategy for spreading risk in deserts, which experience high environmental stochasticity. Finally, Frisch (2002) investigated the survival consequences of spatial and temporal dispersal strategies in cyclopoid copepods from permanent and temporary aquatic habitats and found that both strategies facilitated their persistence.

Thus far we have emphasised similarities between dispersal through space and time, but the two are fundamentally different in some important respects that should lead to different ecological effects, including their potential to rescue declining populations. For example, spatial dispersal to unoccupied habitats can occur, whereas we would expect temporal dispersal to usually be to an established population – as temporal dispersal is just dispersal to a future time at the same location. Thus, spatial dispersal can facilitate the colonisation of empty habitats and influence meta-population dynamics, whereas the effect of temporal dispersal will often be limited to the recolonisation of disturbed habitat (e.g. Mergeay *et al.* 2007), buffering environmental and demographic changes in the local population (but see Cáceres & Soluk 2002; Havel & Shurin 2004). For example, using a simulation approach, Satterthwaite (2010) showed that a genotype adopting a temporal dispersal strategy via dormancy was more likely to recapture a lost site than the non-dormant genotype. Eriksson (1996) also argued that populations characterised by temporal dispersal should be considered a kind of source–sink population where the sources and sinks are temporally related. These observations, among others, led to the concept of *spatial and temporal rescue effects* (see Bohonak & Jenkins 2003). In the context of a meta-population, spatial dispersal reduces the risk of local extinction by maintaining connectivity between populations, resulting in a ‘spatial rescue effect’. In contrast, temporal dispersal reduces the risk of extinction within a population by spreading individuals among different cohorts, leading to a ‘temporal rescue effect’ (Bohonak & Jenkins 2003). These results all reinforce the need to more fully explore the ecological consequences of dispersal syndromes, particularly the consequences for population dynamics and persistence (Duputié & Massol 2013).

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Increased awareness that both dispersal through space and time can spread risk has important conservation and management implications (McPeek & Kalisz 1998). Indeed, many human activities (e.g. farming, logging, fishing) can directly influence the potential for other species to disperse through space and time and, thus, may indirectly affect the persistence of populations. For example, most fish species that experience high harvest rates are characterised by truncated age structure (larger/older individuals are removed via fishing), which directly limits the potential for temporal dispersal, and possibly spatial dispersal (e.g. if older individuals are more prone to migrate). Harvested populations characterised by reduced age complexity have their ‘eggs’ placed in fewer year ‘baskets’, which may reduce their buffering capacity (Perry *et al.* 2010).

Beyond management and conservation of native species, dispersal strategies can also influence the invasion success of non-native organisms. Sol *et al.* (2012) conducted a global comparative analysis of life histories of avian introductions and concluded that ‘the inability to spread the risk over several breeding attempts and/or to delay reproduction if conditions are unfavourable may have important costs’ in terms of invasion success. Recently, Perkins *et al.* (2013) demonstrated the importance of an interaction between life history and dispersal evolution (‘enhanced spatial selection’) for the spread of invasive species. Specifically, by exploring the relative roles of the evolution of life-history traits and spatial dispersal traits on the invasion process, they found that only the joint evolution of life-history traits and spatial dispersal traits could explain the invasion speed of cane toads (*Rhinella marina*) in Australia.

Spatial and temporal dispersal strategies may also play an important role in disease and pest resistance. A prime example comes from the management of the Colorado potato beetle (*Leptinotarsa decemlineata*), the most important defoliator of potatoes in North America, Europe and Asia. Alyokhin *et al.* (2008) showed that Colorado potato beetles adopt a risk-spreading strategy via dispersal through both time and space, which facilitates their expansion and their resistance to insecticides. The authors argued that spatial dispersal may increase the spread of insecticide resistance among geographically isolated fields, especially when emergence from diapause occurs before emergence of potato crops. In addition, they argued that prolonged diapause (up to 3 years) might reduce the efficiency of annual crop and insecticide rotations, as a portion of the beetle population remains dormant and avoids these management techniques only to reappear in the fields in later years (Alyokhin *et al.* 2008).

Recognising how organisms disperse their risk through space and time thus has clear implications for both the conservation of threatened species and the management of natural resources (e.g. harvested fish stocks, agricultural crops). Conservation and management approaches might differ depending on the dispersal traits of the organism (Eriksson 2000). For example, in the case of threatened species with extensive spatial dispersal abilities, management strategies should favour the conservation or restoration of corridors that facilitate connectivity and gene flow among subpopulations. Similarly, in the case of a harvested organism with meta-population structuring, management should consider the importance of spatial dispersal between source and sink populations. In contrast, conservation and management strategies for organisms characterised by strong temporal dispersal should favour the maintenance of life-history diversity that buffers populations (e.g. Greene *et al.* 2010).

CONCLUSIONS AND FUTURE DIRECTIONS

Although the idea that dispersal in space and time are alternative risk spreading strategies was introduced almost half a century ago (Den Boer 1968), our synthesis highlights that this possibility remains poorly appreciated and little studied. We only found 25 theoretical and 18 empirical studies that explored patterns of covariation between spatial and temporal dispersal. While negative covariation between the two dispersal strategies is widely anticipated from theory, more complicated patterns can evolve under various conditions, including autocorrelation in the environment. Because the majority of empirical studies that considered dispersal through space and time have focused on dormancy in plants or diapause in invertebrates (Appendix S2), future work should strategically focus on a broader range of taxa and explore other forms of life-history dispersal that spread risk through time (e.g. iteroparity, Westley *et al.* 2013). Empirical studies focused at different levels of biological organisation – including comparisons among individuals, populations and species (Fig. 3) – underscore the need for an integrated framework that explores risk-spreading trade-offs across levels. Most existing studies have used similar approaches, focused on similar stages of the dispersal process (theory: emigration; empirical: emigration and/or transfer) and focused on similar levels of biological organisation (theory: individual level; empirical studies: species level), stressing the need for studies that span multiple dispersal stages and levels of organisation, and the need for tighter integration between theoretical and empirical studies. Most of the theoretical models reviewed here differ in their assumptions (e.g. different structure of the environment, or type of regulation), but do not capture the complexity of the dispersal process (e.g. trade-offs between the different stages of dispersal; see also Travis *et al.* 2012). The development of eco-evolutionary models that explicitly integrate more complexity should improve our understanding of the causes, consequences and constraints on the evolution of dispersal (Travis *et al.* 2012; Perkins *et al.* 2013). Below we highlight knowledge gaps that are ripe for study and that would help advance the study of dispersal-related life-history syndromes.

- *We need more studies that simultaneously measure both dispersal strategies in nature* to examine the generality of the results presented here. These additional data would allow us to test whether a pattern of negative covariation between dispersal traits is indeed common in the wild (e.g. Appendix S2, Fig. 3), which may improve our ability to predict dispersal (Stevens *et al.* 2013; Whitmee & Orme 2013).
- *We need better measures of dispersal through space and time*. Most empirical studies exploring risk spreading through spatial and temporal dispersal present indirect and qualitative measures of dispersal – e.g. presence or absence of morphological traits that facilitate spatial dispersal or dormancy capable or not for temporal dispersal. Improved measures of dispersal including comparisons of dispersal kernels (e.g. Nathan *et al.* 2012 for review) or utilising recent genetic approaches (e.g. López-Sepulcre *et al.* 2013; Rieux *et al.* 2013; Stevens *et al.* 2013) hold much promise for quantifying both spatial and temporal dispersal.
- *We need to evaluate the relative roles of the environment, constraints, plasticity and natural selection on the covariation between dispersal in space and time*. Such studies are difficult to conduct in nature and require monitoring multiple variables and long-term data sets. The recent development of eco-evolutionary models offers an ideal framework to examine such theoretical concepts (see Travis *et al.* 2012; Perkins *et al.* 2013). This framework allows the integration of the multiple causes, mechanisms and consequences of dispersal syndromes in a unique framework, as well as the empirical information coming from, for example, experimental methods that control environmental conditions and selection (e.g. Beaumont *et al.* 2009; Legrand *et al.* 2012).
- *We need to explore physiological and genetic constraints on dispersal-related life-history traits*. While the role of physiological trade-offs is known to constrain the evolution of dispersal traits (e.g. Zera & Denno 1997), our review also highlights the dearth of studies examining genetic correlations between dispersal through space and time (but see Bégin & Roff 2002), revealing an important limitation for understanding how dispersal strategies evolve (e.g. if multiple dispersal traits are characterised by common genetic basis).
- *We need to understand the magnitude of environmental variability required to select for dispersal through space and time, and how variation in magnitude influences patterns of covariation between dispersal traits*. Environmental conditions experienced by an organism can vary in space (e.g. climatic regions) or in time (e.g. seasonal variation), and can be characterised by the length of favourable and unfavourable periods as well as the frequency and intensity of disturbance events. For example, small and recurrent events (i.e. high frequency, small intensity) may not have the same ecological and evolutionary impacts on organisms as rare events with large magnitude (i.e. low frequency, high intensity; e.g. El Niño). How organisms with different ranges and life histories (especially lifespan) perceive and respond to this environmental variation is important in setting the stage for selection on dispersal traits, but this has not been sufficiently explored.
- *We need to understand the demographic consequences of dispersal syndromes*. While our review focused on documenting the link between spatial dispersal and temporal dispersal, another unexplored area is the influence of these dispersal traits on population growth rate or extinction probabilities (Fig. 4). Understanding the demographic consequences of dispersal-related life-history syndromes should improve our ability to conserve biodiversity and manage pest species and disease outbreaks.
- *We need to better understand geographic variation in dispersal syndromes*. For example, the frequency and intensity of disturbances may differ among geographical regions (e.g. tropical, temperate and arctic regions) leading to possible difference in the magnitude of the covariation expected between dispersal traits across latitudinal gradients, although the limited existing empirical data preclude a test of this possibility. Similarly, organisms may experience different environmental

conditions and selective pressures at range boundaries and during range expansion (e.g. higher environmental unpredictability, less intraspecific competition), leading to possible shifts in the nature of the dispersal syndrome including in the sign and magnitude of correlations between traits (e.g. Burton *et al.* 2010; Hardie *et al.* 2010; Perkins *et al.* 2013). Models that link selection to the evolution of suites of dispersal-related traits hold much promise for elucidating the conditions under which changes in the nature of the dispersal syndrome might arise.

- *We need to understand the evolutionary consequences of dispersal-related life history syndromes*. While we have emphasised similarities in benefits and costs of dispersal in space vs. time, the two are fundamentally different in some important respects – and these differences should lead to different evolutionary effects. For example, one fundamental difference is that dispersal in space regularly brings individuals into different gene pools, whereas dispersal in time may not, at least not to the same extent. Thus, dispersal in time may represent the product of selection on a single population, whereas dispersal in space necessarily involves gene flow among populations that might be adapting to different conditions. For this reason, we expect that local adaptation would select much more strongly against dispersal in space than dispersal in time. This difference also has implications for inbreeding depression – dispersal in space will be much more important for reducing it than dispersal in time. A better understanding of the ecological and evolutionary consequences of dispersal-related life-history syndromes would greatly advance our understanding of the interplay among local adaptation, selection against migrants and population persistence.

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AUTHORSHIP

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