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Quantifying eco-evolutionary contributions to trait divergence in spatially structured systems

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Abstract

Ecological and evolutionary processes can occur at similar time scales and, hence, influence one another. There has been much progress in developing metrics that quantify contributions of ecological and evolutionary components to trait change over time. However, many empirical evolutionary ecology studies document trait differentiation among populations structured in space. In both time and space, the observed differentiation in trait values among populations and communities can be the result of interactions between non-evolutionary (phenotypic plasticity, changes in the relative abundance of species) and evolutionary (genetic differentiation among populations) processes. However, the tools developed so far to quantify ecological and evolutionary contributions to trait changes are implicitly addressing temporal dynamics because they require directionality of change from an ancestral to a derived state. Identifying directionality from one site to another in spatial studies of eco-evolutionary dynamics is not always possible and often not meaningful. We suggest three modifications to existing partitioning metrics so they allow quantifying ecological and evolutionary contributions to changes in population and community trait values across spatial locations in landscapes. Applying these spatially modified metrics to published empirical examples shows how these metrics can be used to generate new empirical insights and to facilitate future comparative analyses. The possibility of applying eco-evolutionary partitioning metrics to populations and communities in natural landscapes is critical as it will broaden our capacity to quantify eco-evolutionary interactions as they occur in nature.

KEYWORDS
community trait change, eco-evolutionary dynamics, partitioning metrics, population trait change, spatial trait variation

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INTRODUCTION

During the past decade ecologists and evolutionary biologists have become increasingly aware that ecological and evolutionary processes can interact to structure populations and communities (Barraclough, 2015; Hairston et al., 2005; Hendry, 2017; Schoener, 2011). This has prompted the development of a suite of metrics to describe and quantify eco-evolutionary contributions to numerous processes that were traditionally considered to result only from ecological dynamics (Collins & Gardner, 2009; Ellner et al., 2011; Govaert et al., 2016; Hairston et al., 2005). These methods, however, have generally been developed for and applied to study changes in populations and communities over time. For example, a study by Becks et al. (2012) used experimental chemostats and a metric developed by Ellner et al. (2011) to show that over a period of 90 days evolutionary responses in the defense traits of an algal prey were more important to rotifer population growth than changes in algal abundance. Another study by Stoks et al. (2016) used an eco-evolutionary partitioning metric to show rapid tracking of change in fish predation pressure by a natural zooplankton population via a mosaic of plasticity, mean trait evolution, and evolution of plasticity. As a last example, a study by Gómez et al. (2016) found that preadaptation to elevated temperature for 48 days in *Pseudomonas fluorescens* contributed as much to change in taxon composition of a compost bacterial community as the presence of the species *P. fluorescens* itself.

Most eco-evolutionary dynamic studies focus on reciprocal evolutionary and ecological changes over time. However, many other evolutionary ecology studies of natural systems consider trait variation among geographically segregated patches and trait turnover along particular spatial gradients rather than over time. Spatial landscape heterogeneity plays a role in shaping genetic structure in natural populations (Ackerman et al., 2013), and the distribution of phenotypes of local populations in a landscape may diverge through adaptive plasticity, local adaptation, and drift (Kawecki & Ebert, 2004; Logan et al., 2016; Lynch, 2007; Via & Lande, 1985). Similarly, species sorting across the landscape might also occur when different environments are dominated by different competing species (Fox & Harder, 2015). Therefore, spatially separated populations or communities may be structured by nonevolutionary (i.e., phenotypic plasticity and species sorting) and evolutionary processes. Quantifying these processes in spatial study systems may improve our understanding of how geographical, environmental, and community features structure evolutionary and nonevolutionary contributions to trait variation in populations and communities inhabiting natural landscapes (e.g., Govaert et al., 2021).

As evolutionary trait change occurs over time, studies quantifying trait evolution often have a clear direction in the observed trait change from past to present. However, studies measuring trait divergence among spatially separated populations or communities capture the trait values of the species at a defined moment in time, reflecting undirected trait differences among spatially separated populations or communities. While the observed trait divergence in these studies does reflect past evolutionary changes, information about past states is often not available. Whether all populations diverged from a common ancestor simultaneously or fragmented at various points throughout the past is often unknown. In such instances, the goal is to quantify the amount of (undirected) trait divergence that can be attributed to evolutionary and nonevolutionary contributions at a single point in time, rather than quantifying these contributions to (directed) temporal trait change that assumes a certain ancestry. Though a handful of eco-evolutionary partitioning metrics are available to quantify ecological and evolutionary contributions to population and community trait change (Ellner et al., 2011; Govaert et al., 2016; Hairston et al., 2005; Price, 1970, 1972), these often assume a known ancestral state or reference. Such information is often not available in spatial study systems, with the exception of studies that investigate invasion history (e.g., stickleback colonization of freshwater lakes) (Bell et al., 2004; Le Rouzic et al., 2011), studies that look at range expansions where the peripheral population can be traced back to more central populations (e.g., Safriel et al., 1994; Swaegers et al., 2014; Volis et al., 2001), or studies that assume an ancestor–descendant relationship (e.g., via space-for-time substitutions) (Etterson & Shaw, 2001).

It is currently unknown to what extent the magnitude of eco-evolutionary contributions to population and community trait change are predictable and repeatable and how much the importance of intraspecific and genetic trait variation is likely to differ across landscapes. Methods that make it possible to quantify ecological and evolutionary contributions to trait variation in spatial landscapes can help to identify spatial structure in these contributions and identify whether the magnitude or relative importance of these contributions is related to features of the organisms (e.g., generation time), the population (e.g., within-population genetic diversity), or the landscape (e.g., degree of isolation or degree of habitat heterogeneity). Moreover, such methods will help to identify when populations and communities are more likely to respond to environmental change in a spatial landscape via shifts in the relative abundances of species, phenotypic plasticity, evolutionary change, or some combination of these. Quantifying context-dependent eco-evolutionary processes is an important next step for studies of eco-evolutionary dynamics.

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Hence, we need appropriate tools to quantify nonevolutionary and evolutionary contributions to population and community trait divergence across landscapes.

In this study, we adapt existing eco-evolutionary partitioning metrics to appropriately accommodate spatially structured (undirected) trait data. Specifically, our study will address the large number of studies that do not seek to understand a trait change across a direction but instead compare trait differentiation among groups. We develop three possible options (referred to as modifications) to existing partitioning metrics developed for temporal data and show that, depending on these modifications, the assessment of the importance or the interpretation of the contributing ecological and evolutionary processes may change. We then explain how to choose between these three options by applying modified metrics to selected empirical data sets. Often the choice will depend on the data collected, the model system used, and the research question. Using empirical examples we illustrate the diversity of research questions that can be addressed and how spatially adjusted metrics can be used to facilitate comparative analyses and generate new empirical insights. Importantly, the modified metrics can also be used to quantify ecological and evolutionary contributions to trait differences among endpoints of experimental treatments, demonstrating the wide scope in which these modified metrics can be used. To better understand the need for adjusted spatially suitable metrics, we first describe the three partitioning metrics we consider in this study and discuss how they are often unable to explicitly address hypotheses for spatially structured study systems.

PARTITIONING METRICS FOR TEMPORAL TRAIT CHANGE

Today, a handful of metrics are available to calculate ecological and evolutionary contributions to average trait change such as the Price equation (Price, 1970, 1972), metrics based on reaction norms (Ellner et al., 2011; Govaert et al., 2016; Hairston et al., 2005), and the recently developed Price-Reaction-Norm (PRN) equation (Govaert et al., 2016). These metrics have previously been compared to one another, with differences in their set of assumptions highlighted (Govaert, 2018; Govaert et al., 2016). The metrics presented here focus on partitioning trait change in a discrete time interval as opposed to trait change in continuous time that can be described by differential equations (see Ellner et al., 2011 for partitioning of continuous-time trait change into ecological and evolutionary contributions).

Price equation

The Price equation, introduced by G. R. Price (Price, 1970, 1972), has been used to describe trait change in a biological population from one generation to the next. The Price equation is very versatile and has proven its usefulness in evolutionary biology (detailed in Queller, 2017), ecology (Fox, 2006; Fox & Kerr, 2012), epidemiology (Day & Gandon, 2006), and evolutionary ecology (Collins & Gardner, 2009; Ellner et al., 2011; Govaert et al., 2016). We here use the version of the Price equation that partitions trait change between two time points in an asexually reproducing population consisting of N genetic lineages, uniquely indexed by $j \in \{1, ..., N\}$ (Govaert et al., 2016). For this metric to apply, it requires information on the relative abundance and average trait value for each genetic lineage (such as genotype, clonal lineage) in each population at both time points. Note that we define genetic lineage as in Govaert et al. (2016), referring to distinct genotypes or clonal lineages. However, any mutation can in principle and by definition result in a different genotype or clonal lineage. In practice, these mutations are not always easily detectable but may still result in phenotypic changes, here then represented by the component "trait change within genetic lineages". There exist many organisms that reproduce asexually and for which the Price equation might be suitable. For example, clonal plants (e.g., *Arabidopsis thaliana*, *Solidago altissima*, North American *Taraxacum officinale*) and seagrasses (e.g., *Zostera marina*) or crustaceans that undergo obligate parthenogenesis (e.g., some morphs of *Daphnia pulex*) are some of the many species for which distinct genetic lineages might differentially assemble into populations and contribute to trait shifts. The Price equation partitions population average trait change between two time points (i.e., $\Delta\bar{z}$) into a component that gives the changes in the relative abundances of the genetic lineages (i.e., genetic lineage sorting) and a component that gives the trait change within genetic lineages:

$$\Delta\bar{z} = \sum_{j=1}^{N} z_2^j \left(q_2^j - q_1^j\right) + \sum_{j=1}^{N} q_1^j \left(z_2^j - z_1^j\right). \quad (1)$$

In this equation, z_k^j (resp. q_k^j) represents the trait value (resp. relative abundance) of genetic lineage j at time t_k.

Reaction norm approach

The reaction norm approach uses the concept of reaction norms originally introduced by R. Woltereck

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("*Reaktionsnorm*"; Woltereck, 1909). Reaction norms have been widely used in quantitative genetics to determine genotype-by-environment interactions. A reaction norm gives a formal association between a phenotype, its genotype, and the environment by mapping each genotype onto its phenotype as a function of the environment (Stearns, 1989). The construction of reaction norms typically involves trait values being collected in two or more distinct environmental conditions. Collecting trait values in a common garden or transplant setting, in which individuals from different populations are assessed in a common environment, makes it possible to detect whether trait differences between populations reflect genetic differences (Lynch et al., 1998). Stoks et al. (2016) and Govaert et al. (2016) used mean reaction norms of a population (i.e., average reaction norm across a representative sample of individuals or genotypes of that population) to assess the contributions of ancestral plasticity, mean trait evolution, and evolution of plasticity to population trait change between two time points. This metric uses population means and partitions the observed trait change between two time points as follows:

$$\Delta\bar{z} = (z_{12} - z_{11}) + (z_{21} - z_{11}) + [(z_{22} - z_{21}) - (z_{12} - z_{11})], \quad (2)$$

where z_{kl} is the average trait value of the population at genetic state k (i.e., sampled at time point t_k) in environmental condition l. This metric thus requires information on the trait values of representative sets of individuals of both populations in the two environmental conditions that correspond to the habitat each population is found in. The first term on the right-hand side of Equation (2) reflects phenotypic plasticity, the second term reflects mean trait evolution, and the last term reflects evolution of plasticity.

Price-Reaction-Norm equation

When reaction norms can be constructed for each genetic lineage and abundances of genetic lineages are available, one can use the Price-Reaction-Norm (PRN) equation, a combination of the Price equation and reaction norm approach, to quantify ecological and evolutionary contributions to population trait change (Govaert et al., 2016). Briefly, this equation partitions population average trait change into genetic lineage sorting, trait change within genetic lineages, phenotypic plasticity, and evolution of phenotypic plasticity. Details on this equation can be found in Appendix S1.

The use of a particular metric often depends on the data collected, and this may depend on the model organism used. For example, the Price and PRN equations require information on both traits and abundances of the genetic lineages within the population. This may be easier to collect for clonally reproducing organisms, such as clonal plants and obligate parthenogenetic crustaceans. In addition, the PRN equation requires that the traits of each genetic lineage are measured in distinct environmental conditions via a common garden or transplant experiment, which then allows for the construction of reaction norms for each genetic lineage. When data on genetic lineages cannot be collected, methods based on reaction norms at the population level can still be used. Here, a population average reaction norm is calculated based on a representative sample of individuals of the population (Ellner et al., 2011; Govaert et al., 2016; Hairston et al., 2005). While the PRN equation, in theory, might be the preferred metric to use due to its more detailed partitioning, it also requires collecting more data. Such data collection might not always be feasible in practice and may be more challenging to collect for sexually reproducing organisms, in which complex breeding experiments would need to be designed in order to collect trait values of particular genetic lineages in common garden experiments.

APPLYING DISCRETE-TIME METRICS TO SPATIALLY STRUCTURED SYSTEMS

Spatially separated populations and communities are structured by ecological and evolutionary processes that may result in trait differentiation among these populations and communities (Fox & Harder, 2015; Kawecki & Ebert, 2004; Logan et al., 2016; Via & Lande, 1985). Spatially separated communities can differ in their trait distributions due to drift, plasticity, and adaptation to local environmental conditions (Kawecki & Ebert, 2004; Logan et al., 2016; Lynch, 2007; Via & Lande, 1985) but also due to a difference in their local species composition (Fox & Harder, 2015). We focus on nonevolutionary processes—phenotypic plasticity at the individual level and species sorting at the community level—combined with evolutionary processes at the population level that can contribute to the mean trait difference observed between spatially separated communities. Moreover, interactions between these ecological and evolutionary processes, such as the evolution of plasticity or between evolution and species sorting, can also contribute to the observed trait differences (Govaert et al., 2016). The previously introduced metrics are designed to evaluate the contributions of these

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ecological and evolutionary processes to discrete-time changes in traits, and this makes them appropriate to explore modifications of these metrics to partition trait differences between spatially separated populations or communities across landscapes. However, most of these discrete-time partitioning metrics, with the exception of the Geber method by Hairston et al. (2005) and Ellner et al. (2011), depend on the choice of the reference (Figure 1a). This dependence on the reference means that when quantifying ecological and evolutionary contributions between two spatially separated populations or communities, partitioning the trait difference from Population 1 or Community 1 to Population 2 or Community 2 using a partitioning metric for directed trait change would produce a different value for the contributing ecological and evolutionary processes than when quantifying these ecological and evolutionary contributions from Population 2 or Community 2 to Population 1 or Community 1. For an example of plastic and evolutionary contributions to trait change from Population 1 to Population 2, and vice versa, using the Price equation, reaction norm approach, and PRN equation, see Figure 2.

Such different results in the contribution of ecology and evolution are an undesirable consequence of applying eco-evolutionary partitioning metrics that are designed to separate directional trait change to sets of populations or communities for which there is no information on their ancestry. We suggest three modifications reflecting three alternative options to convert current partitioning metrics to quantify ecological and evolutionary processes to undirected trait shifts (Figure 1b), typically assessed in spatial study systems. These spatial modifications differ in whether they take a common reference among all populations or communities or just between pairs of populations and communities and whether they partition relative or absolute contributions of ecological and evolutionary processes. Each of these modifications results in the quantification of ecological and evolutionary contributions to undirected trait differentiation. Whereas the choice of a partitioning metric often depends on the type of data collected, the choice of a particular modification will often depend on the research question. In what follows, we describe each modification in detail by providing formulas and demonstrative calculations and explain the meaning of the resulting components. We then apply these modifications to three empirical studies to assist empiricists in choosing which modification is best suited for their research question and model system.

Briefly, a first modification involves setting a common reference (i.e., group reference), which can be done by constructing a midpoint such as the group mean. This is

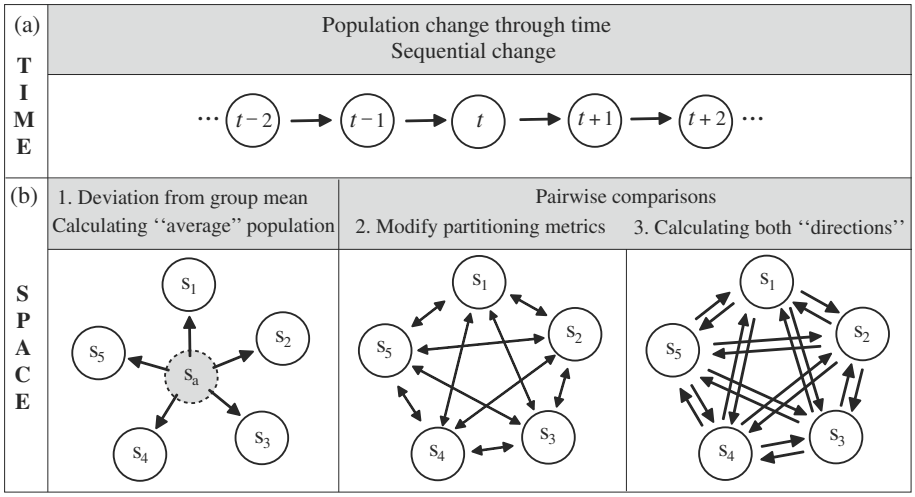

FIGURE 1 Temporal trait change versus spatial trait divergence. Visual representation of (a) directed trait change in temporal study system where trait change occurs between consecutive time points, that is, goes from time point $t - 1$ to t to $t + 1$, and so forth (as indicated by the direction of the arrows) and (b) trait divergence in spatial study systems here consisting of five sites. Ecological and evolutionary contributions to trait divergence can be estimated either as deviations from a common group mean or known ancestor (Modification 1), using partitioning metrics modified to undirected trait change (Modification 2), or as an averaged change between pairs of sites by calculating the ecological and evolutionary contributions from, for example, the population at site s_1 to the population at site s_2, and vice versa, followed by averaging the absolute values of those quantities—and this for all pairwise combinations (Modification 3). In (b), arrows reflect, not spatial distances, but directions of trait divergence for which ecological and evolutionary contributions are calculated. In Modification 1, arrows reflect the calculation from the common reference (s_a, indicated by the gray circle). In Modification 2, arrows reflect the independence of the reference between pairs of populations when calculating ecological and evolutionary contributions. In Modification 3, arrows reflect the calculation of the two directions, in which, for example, population at site s_1 and population at site s_2 are used as a reference in each direction.

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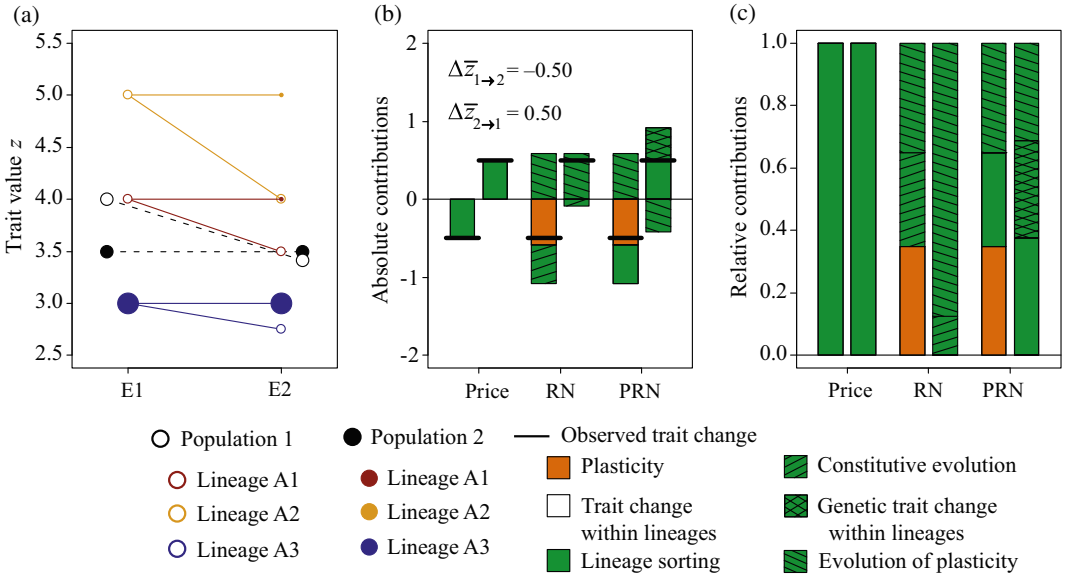

FIGURE 2 Application of temporal partitioning metrics to directed trait change within a pair of populations. Numerical example displaying shift in a trait z between Population 1 at site s_1 (unfilled black circles) and Population 2 at site s_2 (filled black circles), in which the populations consist of the same three genetic lineages (indicated by blue, red, and yellow). The populations differ in environmental condition E, that is, Population 1 at site s_1 (resp. Population 2 at site s_2) originated from an environmental condition E1 (resp. E2). Individuals of the three lineages were measured for trait z in both environmental conditions in order to construct reaction norms. (a) Visualization of reaction norms of the three lineages, where the unfilled (resp. filled) circles represent the average trait value z of the genetic lineage of Population 1 at site s_1 (resp. Population 2 at site s_2) in environmental conditions E1 and E2. The black unfilled (resp. filled) circles represent the average trait value of the total population calculated as a lineage abundance-weighted mean using the lineage trait values and lineage relative abundances (given by the size of the symbols). (b) Absolute and (c) relative contributions of evolutionary and nonevolutionary components to average trait shift from Population 1 to Population 2 ($\Delta\bar{z}_{P_1\to P_2}$) and vice versa ($\Delta\bar{z}_{P_2\to P_1}$) using the Price equation (Price), reaction norm approach (RN), and the PRN equation. In (b) the vertical bar represents the observed trait difference between Population 1 at E1 and Population 2 at E2, calculated as either $\Delta\bar{z}_{P_1\to P_2} = z_2 - z_1$ or $\Delta\bar{z}_{P_2\to P_1} = z_1 - z_2$.

conceptually similar to using Helmert contrasts in regression analysis. This approach partitions trait deviation of each site from the group reference into ecological and evolutionary contributions (Figure 1b). In a second modification, we present versions of the current eco-evolutionary partitioning metrics but that are independent of the reference chosen. In a third modification, we quantify ecological and evolutionary contributions for pairs of populations into directed trait change in both directions (treating each of the populations in each pair as a reference) and then average the resulting fractions (Figure 1b). The main difference between the first and last two modifications is that the second and third modifications result in ecological and evolutionary contributions related to pairs of populations or communities. Hence, the second and third modifications are preferred when one wants to identify whether specific pairs of populations or communities differ in their ecological and evolutionary contributions. The main difference between the second and third modifications is that the third modification only provides relative ecological and evolutionary contributions because it takes the average of the absolute values of the ecological and evolutionary contribution of each direction between two populations or communities, whereas the second modification provides both absolute and relative measures of ecological and evolutionary contributions. Hence, when interested in whether evolution versus ecology act in the same direction, the second modification may be preferred.

We next demonstrate these three modifications for the Price equation (Price, 1970, 1972) and the reaction norm approach (Govaert et al., 2016) because these metrics differ in the type of information they use and their derivation, which can result in slight differences in their spatial extensions. The spatial extensions for the PRN equation, a combination of the Price equation and reaction norm approach, is only briefly mentioned, with details provided in Appendix S1. These metrics can be applied to population as well as community trait data,

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but we here focus on the modification of the metrics applied to populations and provide their extension to community data in Appendix S2.

PARTITIONING METRICS FOR SPATIALLY STRUCTURED SYSTEMS

We describe three modifications to extend directed partitioning metrics to spatial (i.e., undirected) trait data. These can in principle be applied to any data set where researchers are interested in quantifying ecological and evolutionary contributions in a set of spatially separated populations or communities. However, the type of data collected should determine which spatially modified partitioning metric can be used (see Govaert, 2018 for guidelines on the use of partitioning metrics). The main difference between the spatial modifications is how the reference is set, which will alter the interpretation of the ecological and evolutionary contributions calculated. This interpretation may vary from an overall assessment of ecological and evolutionary contributions among spatially separated populations against a common reference to ecological and evolutionary contributions between specific spatially separated populations. The choice of spatial modification may also depend on whether the calculated contributions will be used in further analyses. Then the input required for these analyses might help determine which spatial modification should be used. For example, if calculated contributions for each population would be used further as a response variable in a regression analysis to assess whether these contributions are linked to particular site properties (e.g., environmental gradient or species diversity at a site; for an example see Govaert et al., 2021), then a common reference among spatially separated populations might be the preferred option. However, if one wants to compare contributions to pairwise differences between sites such as genetic distances between populations, then calculating pairwise ecological and evolutionary contributions between spatially separated populations is more preferable. Next, we describe the three different spatial modifications in depth and demonstrate how they apply to the Price equation and the reaction norm approach. We briefly mention the PRN equation, but mathematical details can be found in Appendix S1.

Modification 1: deviation from group reference

The first modification involves setting a common reference (i.e., group reference) by constructing a midpoint, such as a group mean. This is conceptually similar to using Helmert contrasts in regression analysis. Contrasts in regression models determine how the model coefficients of categorical variables are interpreted. Treatment contrasts, for example, set one level as reference and compares all subsequent levels to this reference. Helmert contrasts, however, compare each level against a mean of the preceding levels, and scaling the contrasts can allow the comparison of two binary treatment levels to their midpoint (average). Depending on the baseline, interpretation of the model coefficients change. Eco-evolutionary partitioning among spatially separated populations can in a similar way be performed by using the same reference for comparisons with all observed populations by setting a group reference. This group reference could reflect a known ancestral state (e.g., when a mainland population invades several islands) or a control treatment in a laboratory experiment. If no such information is available, one could also calculate a group mean by constructing an average population. Because ecological and evolutionary contributions can then be calculated with a clear direction from the group reference to each of the subsequent populations, one can use the temporal version of the Price equation and the reaction norm approach to calculate eco-evolutionary deviations from this group reference (e.g., the group mean) for each observed population. Constructing a group mean by constructing an average population can differ depending on the type of metric and, thus, data used, and we therefore show how this average population can be constructed when using data applicable to the Price equation, the reaction norm approach, or PRN equation (the latter detailed in Appendix S1).

Price equation

We here assume a set of m spatially separated populations in which each population consists of the same N genetic lineages from which we have information on the relative abundances and trait values. While this assumption might be unlikely in natural landscapes consisting of spatially separated populations, it is used here to facilitate illustration of the procedure. A detailed explanation of when this assumption is not met (i.e., when sites differ in the presence and absence of genetic lineages) is given in Appendix S3. Constructing a group mean requires calculating average trait values (z_a^j) and average relative abundances (q_a^j) of the genetic lineages across the populations, which are calculated as follows:

$$z_a^j = \frac{1}{m}\sum_{k=1}^{m} z_k^j \quad \text{and} \quad q_a^j = \frac{1}{m}\sum_{k=1}^{m} q_k^j, \tag{3}$$

where z_k^j and q_k^j denote the average trait value and relative abundance of genetic lineage j of Population k. Using

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the Price equation, we can partition the observed population trait deviation of Population k from the group mean or average population (P_a) as follows:

$$\Delta\bar{z}_{P_a \to P_k} = \sum_{j=1}^{N} z_k^j \left(q_k^j - q_a^j\right) + \sum_{j=1}^{N} q_a^j \left(z_k^j - z_a^j\right). \quad (4)$$

The first term on the right-hand side of Equation (4) refers to the trait deviation due to genetic lineage sorting, and the second term refers to the trait deviation due to within-lineage trait deviation.

Reaction norm approach

The construction of a group mean in the reaction norm approach can be seen as an average population assumed to originate from an average environmental condition (see Appendix S4 for a graphical explanation on how to create this group mean). In this case, we assume that the set of m populations can be subdivided into two subsets based on an environmental condition (e.g., populations in which a specific predator is present or absent or populations experiencing high or low nutrients). We further assume that the traits of each population have been measured in a common garden or transplant experiment in the respective two environmental conditions. To construct this group mean, we need to calculate z_{al} (i.e., the average trait value of the average population in environmental condition $l \in \{1, 2\}$), z_{ka} (i.e., the average trait value of Population k in the average environmental condition a), and z_{aa} (i.e., the average trait value of the average population in the average environmental condition a) as follows:

$$z_{al} = \frac{1}{m}\sum_{k=1}^{m} z_{kl}, \quad z_{ka} = \frac{1}{2}\sum_{l=1}^{2} z_{kl} \quad \text{and} \quad z_{aa} = \frac{1}{m}\sum_{k=1}^{m} z_{ka}. \quad (5)$$

The group mean thus reflects an average population living in average environmental conditions. The average environmental condition might in some cases be considered artificial, for example, when the average environment reflects neither the presence nor the absence of predation or represents conditions that are actually very rare in the landscape. The reaction norm equation can then be used to partition the observed trait deviation of Population k from the group mean or average population (P_a) as

$$\Delta\bar{z}_{P_a \to P_k} = (z_{al} - z_{aa}) + (z_{ka} - z_{aa}) + ([z_{kl} - z_{ka}] - [z_{al} - z_{aa}]). \quad (6)$$

The first term on the right-hand side of Equation (6) is the plasticity component, the second term is the trait deviation due to genetic trait differentiation, and the third term is the trait deviation due to a genetic differentiation in plasticity. It is important to keep in mind that the plasticity component reflects not the absolute amount of plasticity but rather the average phenotypic plasticity response. Note that as the last component on the right-hand side of Equation (6) approaches zero for a certain Population k, the more similar degree of plasticity the population has with the average plasticity. The greater this value is, the more genetically differentiated the population is in its plasticity response compared to the group mean (i.e., the average population).

We here illustrated the application of the reaction norm approach when m spatially separated populations can be divided into two subsets linked to two distinct environmental conditions (i.e., $l \in \{1, 2\}$, e.g., absence or presence of predation, low or high nutrient concentration). However, the reaction norm approach can also be used when there are more than two environmental conditions and, thus, where the spatially separated populations can be divided into more than two subsets linked to environmental conditions (i.e., $l \in \{1, ..., n\}$). As with the two environmental conditions, one requires that the traits of each population be measured in a common garden or transplant experiment in the respective (here n) environmental conditions in order to calculate the components in Equation (5), in which the sum for z_{ka} would be calculated over n instead of two environments, that is,

$$z_{ka} = (1/n)\sum_{l=1}^{n} z_{kl}.$$

Price-Reaction-Norm equation

The PRN equation assumes information available on the abundances and reaction norms of genetic lineages of the different spatially separated populations. Constructing a group mean involves calculating average trait values for each genetic lineage j that are assumed to belong to an average population in the two environmental conditions (detailed in Appendix S1). One then uses the PRN equation for directed temporal trait change to calculate the contributions of plasticity, trait deviation due to lineage sorting, trait deviation due to genetic trait differentiation, and trait deviation due to genetic differentiation in plasticity to trait shifts from the average population to each of the m spatially separated populations (Appendix S1: Equation S3).

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Modification 2: partitioning metrics for undirected trait change

In the first modification, we constructed a common reference from which ecological and evolutionary contributions to the trait shift from the reference to each population could be calculated. Such a group reference can reflect a common ancestral state, a control treatment from a laboratory experiment, or a group mean. The group mean can be calculated as an average population among the set of spatially separated populations. The construction of such a common reference makes it possible to compare the quantified ecological and evolutionary contributions across populations. However, it still uses the metrics designed for directed trait change. In this modification, we propose a version of the Price equation, reaction norm approach, and PRN equation that is independent of the reference. This means that when calculating ecological and evolutionary contributions from Population 1 to Population 2 or from Population 2 to Population 1, the spatially modified metric gives the same contribution of ecology and evolution independent of whether Population 1 or Population 2 was used as a reference. This differs from the first modification, in which ecological and evolutionary contributions depend on the choice of reference. We next show how this modification applies to the Price equation and the reaction norm approach for a pair of populations, which we denote as Population 1 and Population 2. We briefly mention the PRN equation but provide full details in Appendix S1.

Price equation

The Price equation can be used to separate trait change between populations into a lineage sorting and a within-lineage trait change component. Depending on whether we partition the trait change from Population 1 to Population 2 (as in Equation 1) or from Population 2 to Population 1, given by

$$\Delta\bar{z}_{P_2\to P_1} = \sum_{j=1}^{N} z_1^j\left(q_1^j - q_2^j\right) + \sum_{j=1}^{N} q_2^j\left(z_1^j - z_2^j\right), \quad (7)$$

the contribution of lineage sorting equals the difference in relative abundances of the genetic lineages between both populations multiplied by the trait value of the genetic lineages of either Population 1 (z_1^j) as given in Equation (7) or of Population 2 (z_2^j) as given in Equation (1). These two terms thus only differ in the trait value that is multiplied by the change in relative abundances of the genetic lineages. Multiplying this term instead by an average genetic lineage trait value $(z_1^j + z_2^j)/2$ as opposed to the genetic lineage trait value of either Population 1 or 2, would result in a component of lineage sorting independent of the reference population. Similarly, the within-lineage trait change component—the second term in Equations (1) and (7)—equals the difference in the trait values of the genetic lineages and only differs in its multiplication by the relative abundances of Population 1 (q_1^j) as given in Equation (1) or of Population 2 (q_2^j) as given in Equation (7). It can be made independent of the reference using the average relative abundance of the genetic lineages of the two populations. This results in a spatial version of the Price equation that is independent of the reference chosen. Hence, when using this version of the Price equation to calculate the contributions of ecology and evolution between two populations, one will get the same relative contributions of ecology and evolution independently of whether one partitions change from Population 1 to Population 2, or vice versa. The spatially modified version of the Price equation thus partitions the observed trait divergence between two spatially separated populations as

$$\Delta\bar{z} = \sum_{j=1}^{N}\left(\frac{z_1^j + z_2^j}{2}\right)\left(q_2^j - q_1^j\right) + \sum_{j=1}^{N}\left(\frac{q_1^j + q_2^j}{2}\right)\left(z_2^j - z_1^j\right). \quad (8)$$

The first term on the right-hand side of Equation (8) quantifies the observed trait divergence due to differences in the relative abundances of the genetic lineages between the two populations, and the second term quantifies the observed trait divergence due to differences in trait values within genetic lineages.

Reaction norm approach

A version of the reaction norm approach suitable for undirected trait shifts was developed by Hairston et al. (2005) and Ellner et al. (2011). This metric is often referred to as the Geber method. Originally, Ellner et al. (2011) used this metric to quantify the ecological (impact of an environmental factor) and evolutionary (impact of the genetic component of a trait) contribution to the change in an ecological response variable (e.g., population growth). However, this metric can also be used to partition the shift in a phenotypic trait z between two populations into main effects of ecology and evolution, that is,

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$$\Delta\bar{z} = \frac{1}{2}[(z_{12} - z_{11}) + (z_{22} - z_{21})] + \frac{1}{2}[(z_{21} - z_{11}) + (z_{22} - z_{12})]. \quad (9)$$

As in the reaction norm approach, z_{kl} represents the trait value of the population at time t_k or site k in environmental condition l. The components in Equations (2) and (9) can be found by solving the least-squares normal equations of a linear regression model with and without an interaction component (Govaert, 2018) and are equivalent to the main effects in an analysis of variance (ANOVA) (Ellner et al., 2011; Hairston et al., 2005). In the regression model, the trait z is included as a response variable against two indicator variables, reflecting the genetic state (given by k in Equation 9) and ecological state (given by l in Equation 9) of the population.

Besides the fact that the reaction norm approach by Govaert et al. (2016), given in Equation (2), depend on the reference, while the approach by Ellner et al. (2011) does not, another key difference between Equations (9) and (2) is that the approach presented by Ellner et al. (2011) does not subdivide evolution into a component of mean trait evolution and a component of evolution of plasticity. The interpretation of the components of both approaches is thus different. The first term on the right-hand side of Equation (9) sums the trait change in Population 1 (first part of the first term) and Population 2 (second part of first term) due to a change in environmental condition from Environment 1 to Environment 2 divided by two and can be seen as an average plasticity effect. The second term in Equation (9) sums the trait change in Environment 1 (first part of second term) and Environment 2 (second part of second term) between both populations divided by two and can be seen as an average effect of genetic trait differentiation. This metric thus only estimates the average effects of genetic trait differentiation and environmental plasticity and does not capture the full spectrum of evolutionary change (cf. evolution of plasticity is likely half included in each of the evolutionary and environmental components; Ellner et al., 2011). However, the advantage of this equation is that the contributions of evolution and ecology to the trait change from Population 1 to Population 2 are equal in magnitude but opposite in sign to the contributions of evolution and ecology to the trait change from Population 2 to Population 1. Hence, the contributions of evolution and ecology for this metric are independent of whether one partitions trait shift from Population 1 to Population 2 or vice versa (and thus independent from the reference). This metric is thus very suitable for quantifying evolutionary and nonevolutionary contributions to spatially (undirected) trait shifts, at least if the quantification of the genetic differentiation of plasticity is less important.

Nevertheless, it is possible to include a component to quantify genetic differentiation in phenotypic plasticity between spatially separated populations for Equation (9). This can be done by solving the least-squares normal equation for the model coefficients of a linear regression model with interaction term, but setting the contrasts to Helmert contrasts (e.g., Pantel et al., 2015). To evaluate trait deviations from a midpoint, Helmert contrasts are used, as opposed to treatment contrasts, which would take one of the genetic and ecological state as a baseline. This then results in the following formulas linked to an average phenotypic plasticity effect, an average effect of genetic trait differentiation, and an average effect of genetic differentiation in phenotypic plasticity:

$$\begin{aligned}
&\text{Phenotypic plasticity}: \frac{1}{2}[(z_{12} - z_{11}) + (z_{22} - z_{21})],\\
&\text{Genetic trait differentiation}: \frac{1}{2}[(z_{21} - z_{11}) + (z_{22} - z_{12})],\\
&\text{Genetic differentiation in plasticity}: \frac{1}{2}[(z_{22} - z_{21}) - (z_{12} - z_{11})].
\end{aligned} \quad (10)$$

A disadvantage of adding this interaction component is that the sum of these three components does not add up to the observed trait shift (i.e., $\Delta\bar{z}$).

Price-Reaction-Norm equation

The PRN approach combines features of the Price equation and the reaction norm approach, so the spatially modified version of the PRN equation for undirected trait shifts combines elements from the version of the Price equation and of the reaction norm approach for undirected trait shifts. Briefly and in words, in the PRN equation for undirected trait shifts, the lineage sorting component is weighted by the average trait value of genetic lineages, whereas the phenotypic plasticity and evolutionary components are weighted by average abundances of the genetic lineages, similarly as in the Price equation (detailed in Appendix S1). Because the PRN equation contains the plasticity and evolutionary components of the version of the reaction norm approach for directed trait shifts, we substitute these components with the average plasticity and average evolution components given in Equation (9) to construct a version of the PRN equation for undirected trait shifts (Appendix S1: Equation S6).

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Modification 3: average of components in both directions

From the second modification we obtain a version of the Price equation, the reaction norm approach, and the PRN equation for undirected trait shifts. Such modification may not always be straightforward or possible, as we saw for the reaction norm and PRN approach. We therefore propose a third modification when a straightforward modification of the metric is not possible. Here we quantify the contribution of ecological and evolutionary processes to trait shifts between pairs of populations by calculating the contributions twice when treating each population in the pair as a reference. We then calculate the average of each contribution within the pair.

For instance, consider two populations inhabiting spatially distinct sites (referred to as Population 1 and Population 2). One could calculate contributions of ecological and evolutionary processes to the trait shift between Population 1 and Population 2 (i.e., $\Delta\bar{z}$), using a metric of directed temporal trait change and by first using Population 1 as a reference ($\Delta\bar{z}_{P_1\to P_2}$), and then calculate contributions of similar processes but instead using Population 2 as a reference ($\Delta\bar{z}_{P_2\to P_1}$). Treating each population as a reference relates to the contributions calculated in the hypothetical example displayed in Figure 2b. To calculate the average of each ecological and evolutionary component, we then take the average of the absolute values of the ecological and evolutionary components obtained from each calculation. Note that we use absolute values because the total effect of ecological and evolutionary contributions would be reduced when the contributions of each direction are opposite in sign and added together. We next formulate how this modification translates for the Price, reaction norm, and PRN equation (the latter detailed in Appendix S1) when assuming pairs of spatially separated populations (in what follows, the populations used in the pairwise comparison are stated as Population 1 and Population 2).

Price equation

The Price equation given by Equations (1) and (7) assumes Population 1 and Population 2 to be the references, respectively. Both equations partition the observed trait shift between Population 1 and Population 2 for a trait z into ecological and evolutionary contributions. The first term on the right-hand side of Equations (1) and (7) gives the change in the relative abundances of the lineages. These two terms only differ in the trait value that is multiplied by the change in relative abundances of the genetic lineages, which is either z_2^j in Equation (1) or z_1^j in Equation (7). Averaging the absolute values of these two terms gives the overall magnitude of lineage sorting to the trait divergence between Populations 1 and 2, that is,

$$\frac{\left|\sum_{j=1}^{N} z_2^j\left(q_2^j - q_1^j\right)\right| + \left|\sum_{j=1}^{N} z_1^j\left(q_1^j - q_2^j\right)\right|}{2}. \quad (11)$$

Similarly, one can calculate the overall magnitude of the trait difference within genetic lineages by averaging the absolute values of the two last terms in Equations (1) and (7), that is,

$$\frac{\left|\sum_{j=1}^{N} q_1^j\left(z_2^j - z_1^j\right)\right| + \left|\sum_{j=1}^{N} q_2^j\left(z_1^j - z_2^j\right)\right|}{2}. \quad (12)$$

To obtain the overall relative importance of each process, one can then use the outcomes of the components given by Equations (11) and (12) and divide them by their sum.

Reaction norm approach

The reaction norm approach given in Equation (2) partitions observed population trait change from one time point to the next into ancestral plasticity, mean trait evolution, and evolution of plasticity. For two spatially separated populations, however, we can calculate the different components using either Population 1 or Population 2 as reference. Partitioning trait divergence from Population 1 to Population 2, hence using Population 1 as a reference, is given by Equation (2). When using Population 2 as a reference, the observed trait difference equals $\Delta\bar{z}_{P_2\to P_1} = z_{11} - z_{22}$ and can be partitioned into the following components:

$$\Delta\bar{z} = (z_{21} - z_{22}) + (z_{12} - z_{22}) + [(z_{22} - z_{21}) - (z_{12} - z_{11})]. \quad (13)$$

The first term on the right-hand side of Equation (13) is the plasticity response of Population 2, the second term is the genetic trait differentiation from Population 2 to 1, and the last term gives the genetic differentiation in plasticity from Population 2 to 1. Averaging the absolute value of the plasticity components of Equations (2) and (13) then gives the absolute magnitude of plasticity to the trait difference between Population 1 and 2:

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$$\frac{|z_{12}-z_{11}|+|z_{21}-z_{22}|}{2}. \quad (14)$$

Equation (14) differs from the average plasticity component of Equation (10) in its second term. However, when $z_{12} \geq z_{11}$ and $z_{22} \geq z_{21}$, this and the previous modification give the same contribution for the average plasticity component. Similarly, averaging the genetic trait differentiation components and the genetic differentiation in the plasticity components of Equations (2) and (13) gives the absolute magnitude of genetic trait differentiation:

$$\frac{|z_{21}-z_{11}|+|z_{12}-z_{22}|}{2}. \quad (15)$$

The same contribution will be found as in Equation (10) when $z_{21} \geq z_{11}$ and $z_{22} \geq z_{12}$. Lastly, because the genetic differentiation in plasticity is the same in both directions, the average of the absolute values of genetic differentiation in plasticity in both directions equals the absolute value of one direction:

$$|[(z_{22}-z_{21})-(z_{12}-z_{11})]|. \quad (16)$$

Price-Reaction-Norm equation

For the PRN equation we can average the absolute values of the contributions of lineage sorting, genetic trait differentiation within genetic lineages, genetic differentiation in plasticity within genetic lineages, and the phenotypic plasticity obtained from a partitioning of the trait shift from Population 1 to Population 2, and vice versa (Appendix S1: Equation S7).

In this modification, we chose to sum the absolute values of the ecological and evolutionary terms of each direction (i.e., the ecological and evolutionary terms obtained from partitioning the population trait difference from Population 1 to Population 2 and from Population 2 to Population 1), so that the overall total effect of each component reflected the absolute magnitude of change (and not the reduced value that would result if a change of terms were in opposite directions for each component and the absolute values were not taken). This was one way to resolve the issue, but others are possible. For example, one can also take the difference between the ecological and evolutionary terms of each direction and divide this difference by 2. Applying this to the Price equation would, for example, mean removing the absolute values in the terms given in Equations (11) and (12) in Modification 3 and then subtracting these terms from each other (as opposed to taking their sum). Interestingly, this gives the same modified version of the Price equation as we found for Modification 2 (Equation 8). However, using this alternative approach (no absolute value, subtraction) for the reaction norm and PRN equation would not create an equivalent with their counterparts in Modification 2 (i.e., Equation 9; Appendix S1: Equation S6), unless the genetic differentiation of plasticity component is omitted. As we mentioned when articulating Modification 2, this modification therefore does not quantify the contribution of genetic differentiation of plasticity. For this reason, taking the sum of the absolute values of the ecological and evolutionary contributions of each direction instead of the subtraction approach makes it possible to estimate the total relative contribution of each component, including the genetic differentiation of plasticity, to the observed trait difference between two spatially separated populations. Nevertheless, having these two approaches to solving the same problem shows that there are potentially many ways to construct spatially modified eco-evolutionary partitioning metrics that may be equivalent in some instances.

APPLICATION TO EMPIRICAL EXAMPLES

We next demonstrate applications of spatially modified partitioning metrics to a set of empirical studies. Because we wish to demonstrate spatial modifications, we focus on those spatial studies where one cannot imply a straightforward direction to the trait change. Examples of spatial study systems that do consider a directed trait change among spatially separated populations include investigations of invasion history (e.g., stickleback colonization of freshwater lakes) (Bell et al., 2004; Le Rouzic et al., 2011), range expansions where the peripheral population can be traced back to more central populations (e.g., Safriel et al., 1994; Swaegers et al., 2014; Volis et al., 2001), and studies using space-for-time substitutions to evaluate, for example, climate change (i.e., studies that infer temporal trends from populations that differ in age or in some temporally associated sequence) (e.g., Etterson & Shaw, 2001; Blois et al., 2013). A worked-out example of applying partitioning metrics to a directed spatial study of Etterson and Shaw (2001) can be found in Appendix S5.

Here, we apply spatially modified partitioning metrics to three studies to answer questions on how variation in selection pressure can alter ecological and evolutionary contributions and whether ecological and evolutionary contributions differ in time and space. In a first application to evolving metapopulations of salamander larvae of *Ambystoma*

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maculatum, we determine whether contributions of plasticity and evolution depend on the selection pressure experienced (data obtained from Urban, 2008). In a second application, we determine whether zooplankton *Daphnia* spp. vary in their evolutionary and nonevolutionary responses to experimental environmental variation (data obtained from Weider et al., 2008). Last, we compare eco-evolutionary responses in two studies that evaluated a similar selection pressure, the addition of a predator species, to *Daphnia magna* in an experimental and a natural setting, to assess whether trait divergence in time and space can be structured by the same ecological and evolutionary processes (data obtained from De Meester, 1996 and Cousyn et al., 2001). The first and third examples use data on spatially separated populations. However, in the second example, we compare distinct experimental treatments. With this example, we want to illustrate that the modified metrics for undirected trait shifts can also be used to quantify ecological and evolutionary contributions to trait shifts between experimental treatments in which no direction of the trait shift is implied.

Example 1: do relative contributions of plasticity and evolution vary depending on the selection pressure experienced?

Spatial partitioning metrics can be used to determine whether the contribution of ecology and evolution varies under different selection regimes. We used data from a metapopulation of *A. maculatum* larvae originating from habitats with and without its predator *Ambystoma opacum* (Urban, 2008). *A. maculatum* are North American salamanders whose larvae develop in ponds. In some ponds, *A. maculatum* larvae are predated by larvae of the marbled salamander *A. opacum*. From the metapopulation we had 18 *A. maculatum* populations varying in predator presence. For each of these populations, measurements of larval body mass were assessed in a laboratory experiment using a control and predator kairomone condition, which allows the construction of reaction norms (Figure 3a). Specifically, we wanted to assess whether populations originating from a predator-free environment differed in their plastic and genetic response compared to populations from a predator environment. We therefore decided to construct a group mean and assess the contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity to shifts in larval body mass from this group mean to each of the 18 populations using the reaction norm approach. Figure 3c,d shows two alternative ways of visualizing these results. If a division in groups of populations (here: those with and without predators) can be made, boxplots can be used to visualize differences in the relative contributions of the components between the two groups (Figure 3c). However, one can also visualize the results in a triangle plot, which shows the individual values of the relative contribution of the three components for all 18 populations (Figure 3d).

Using different symbols for populations that originate from habitats with and without a predator illustrates how these two groups differ in contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity to their trait deviation from the mean. Overall, plasticity contributed most to the observed deviations in mean prey body mass across the metapopulation, whereas genetic differentiation in plasticity had the smallest relative contribution. After categorizing the 18 populations by whether or not they came from habitats with or without predation, we found that genetic differentiation in prey body mass varied significantly more in populations where a predator was present compared to populations without predators (Levene's test: $F_{1,16} = 10.06$, $p = 0.006$) (Figure 3c) and that the relative contribution of genetic differentiation in plasticity to body size was significantly larger in larvae originating from sites with predators compared to larvae from sites without predators (*t*-test: $t_{16} = -2.21$, $p = 0.042$) (Figure 3b). The narrow range in the relative contribution of genetic trait differentiation in prey body mass of the predator-free populations is depicted in the triangle plot by the gray zone (Figure 3d).

We here decided to construct a group mean because we wanted to have a common reference when comparing populations from a predator-free and predator environment. However, one could also have asked how repeatable contributions of plasticity and evolution to trait shifts are when comparing an average predator-free *A. maculatum* population to each individual *A. maculatum* population coexisting with a predator. Alternatively, one could also have compared all pairs of predator-free and predator-present populations and calculate contributions of plasticity and evolution between each pair. These questions would use different populations as reference than were used in the example presented here, and we present those analyses in Appendix S5.

Example 2: do relative contributions of clonal sorting and phenotypic plasticity vary among species and treatments?

In the previous example we assessed whether contributions of plasticity and evolution differed among varying selection pressures. However, such contributions may not only depend on the ecological condition but also vary among species. In this example, we used the study by Weider et al. (2008) to quantify among-species variation in

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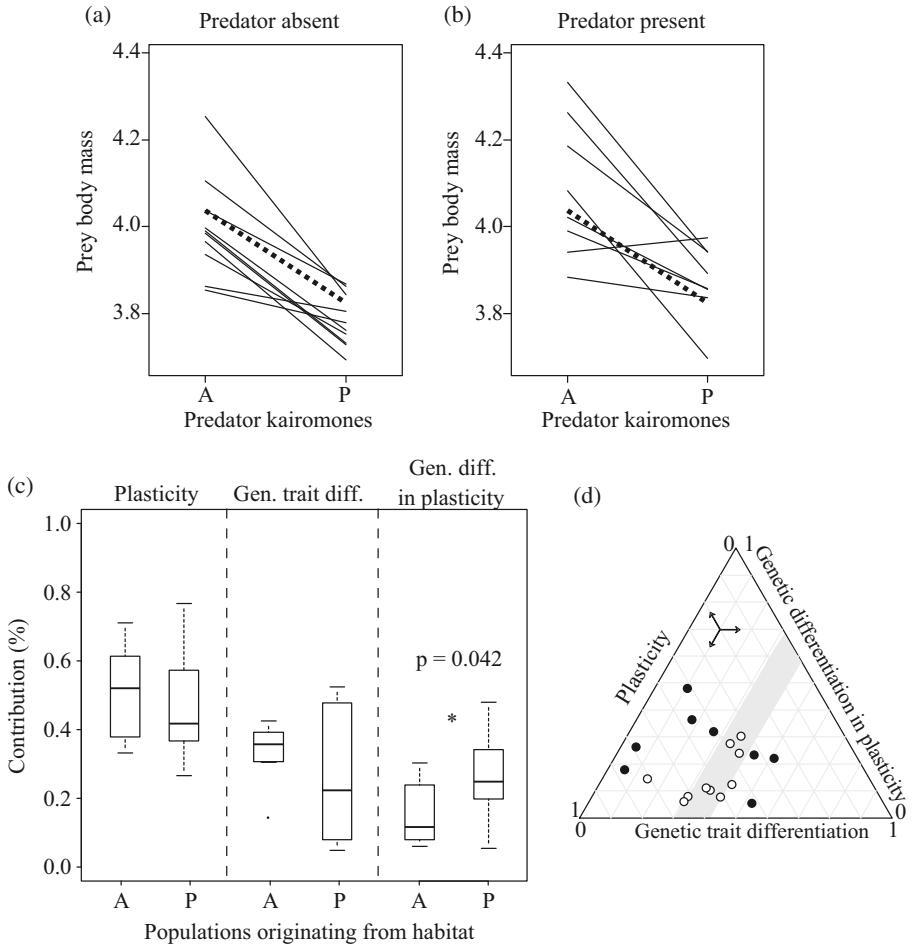

FIGURE 3 (a, b) Reaction norms for larval body mass of 18 populations of *Ambystoma maculatum* originating from sites where predator *A. opacum* is either present or absent. Body masses of larvae were measured in absence (A) and presence (P) of predator kairomones. The dashed black line gives the group mean for all 18 populations. (c) Boxplots of relative contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity relative to deviation in mean larval body mass using the reaction norm approach as described in Modification 1. Results are presented separately for the populations originating from habitats without (A) and with (P) the predator *A. opacum*. (d) Triangle plot showing relative contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity. Filled (resp. unfilled) circles represent the *A. maculatum* populations originating from sites where the predator *A. opacum* is present (resp. absent). Data were extracted from fig. 3 in Urban (2008). Arrows on the triangle plot indicate how to read the coordinates of the points on the graph by following the direction indicated by the arrow.

nonevolutionary and evolutionary contributions to shifts in age at first reproduction in an experiment involving three species of *Daphnia* cultured in a full-factorial design of high and low food quality and quantity. Trait values of two clones for each species were measured in a common garden with four food conditions: low-quality low-quantity (LL), high-quality low-quantity (HL), low-quality high-quantity (LH), and high-quality high-quantity (HH). Species were inoculated together in the four food conditions, and the densities of clones and species were followed in a 90-day microcosm experiment. Because we wanted to assess the effect of each food condition for the relative importance of ecological and evolutionary processes and whether these varied among species, we constructed a group mean for each species as a common reference across the four food conditions. Since we have information on clonal frequencies and clonal trait values in varying food conditions (allowing the construction of reaction norms), we decided to use the PRN equation. However, because we had clonal trait values only at the beginning of the experiment and not at subsequent time points, we had to make the assumption that clonal trait values do not change. We therefore could not assess genetic trait differentiation and genetic differentiation in plasticity for this study. Therefore, the PRN equation reduces to the Price equation with interaction component. Using this metric, we can assess the contributions of lineage sorting, within-lineage trait differentiation

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(here due to phenotypic plasticity), and their interaction to deviations in age at first reproduction for three *Daphnia* species (*D. pulex*, *D. pulicaria*, and their hybrid) for the four aforementioned food conditions (LL, HL, LH, HH). We used clonal frequencies at Day 30 of a 90-day microcosm experiment because species were outcompeted later in the experiment, and our goal was to compare across species.

By plotting the trait deviation from the average due to lineage sorting, within-lineage trait differentiation, and their interaction across treatments and species, we were able to detect whether species varied in the relative importance of these components for the observed response to the experimental treatments and whether this variation among species differed among food conditions (Figure 4). Overall, we found that within-lineage trait differentiation was the largest contributor (Figure 4). The contributions of lineage sorting, within-lineage trait differentiation and their interaction were in opposite directions in the LL and HH treatments for all species except *D. pulicaria*. *Daphnia pulex* and the hybrid species showed similar directions of the contributions for lineage sorting and within-lineage trait differentiation, where lower food quality was in opposite direction to high food quality conditions. By applying partitioning metrics to different species, we found that species varied in how the components were associated among treatments, indicating that different species may use different combinations of ecological, evolutionary, and eco-evolutionary processes to respond to environmental variation (in this instance food quantity and quality).

Example 3: are spatial and temporal trait divergence structured by the same processes? a case study in *daphnia*

Selection pressures can vary similarly over time and across locations in space. Determining whether ecological and evolutionary contributions to trait shifts to the same selection pressure over time and in space are achieved through similar combinations becomes possible with spatially modified partitioning metrics and existing temporal partitioning metrics. We here address this by comparing eco-evolutionary responses of *D. magna* phototactic behavior to predators using the studies of De Meester (1996) and Cousyn

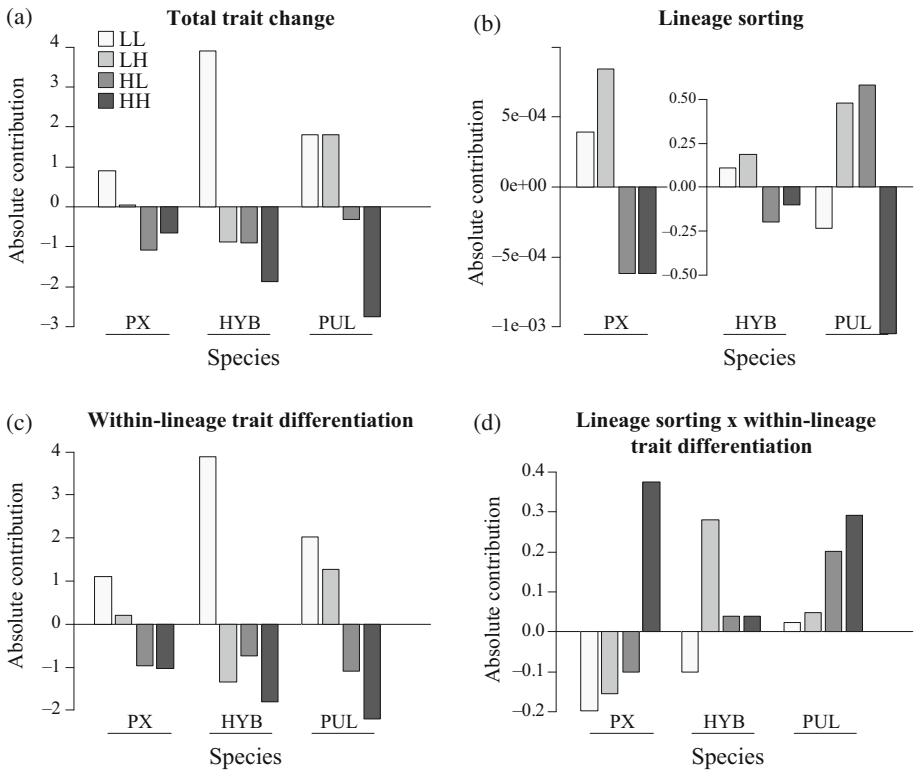

FIGURE 4 Graphical visualization of (a) total trait deviation from group mean calculated across treatments for each species (PX: *Daphnia pulex*, PUL: *Daphnia pulicaria*, and HYB: their hybrid) and treatment (low-quality low-quantity [LL], low-quality high-quantity [LH], high-quality low-quantity [HL], and high-quality high-quantity [HH]) and the absolute contributions of (b) shifts in lineage composition, (c) trait differentiation within lineages, and (d) their interaction using PRN approach.

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et al. (2001). These studies used common garden experiments to measure phenotypic responses in phototactic behavior to different fish predation pressures (i.e., none, low, and high) for three *D. magna* (sub)populations in space and time (resurrection ecology approach), exposing different *D. magna* clones from each (sub)population to a fish kairomone (mimicking high fish predation pressure) and a control (absence of fish predation threat) treatment. These data sets were previously used to illustrate the similarity of responses in phototactic behavior in space and time by Freeman and Herron (2007). Because these studies used the same model system with similar selection pressures experienced and measured traits in a similar way, we can investigate whether the resulting eco-evolutionary contributions to the observed trait shifts are similar in space and time.

From the temporal study Cousyn et al. (2001) we know that the *D. magna* population underwent changes in phototactic behavior from a period of no fish to high fish predation pressure and from a period of high fish to reduced fish predation pressure. To represent this temporal shift in predation pressure, we therefore compared only those spatial populations experiencing the selection pressure corresponding to the temporal shift. Thus, for the study of De Meester (1996), we compared the spatial *D. magna* population of Citadelpark (fishless pond) with that of Lake Blankaart (high-fish-predation pond) and the spatial *D. magna* population of Lake Blankaart with that of Driehoeksvijver (reduced-fish-predation pond). From the common garden experiments performed in Cousyn et al. (2001) and De Meester (1996), reaction norms of phototactic behavior can be constructed for each (sub)population (Figure 5a,b), allowing the use of the reaction norm approach. We used the spatial modification of a nondirectional version of the reaction norm approach (developed by Ellner et al., 2011), however, with an interaction component to quantify contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity between the previously mentioned pairs of populations (Figure 5c). The use of the same metric in both studies allows comparing the evolutionary and ecological contributions to observed trait shifts in time and space. Comparison of contributions between studies was done using a bootstrap analysis resampling the data with replacement and recalculating the contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity. We then compared the 95% confidence intervals of the relative (Figure 5c) and absolute (Figure 5d) contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity between pairs of (sub)populations that experienced similar fish predation pressure. We found that all 95% confidence intervals obtained from the bootstrapping overlapped for the absolute contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity, indicating a similar range of the absolute contributions of these processes between pairs of (sub)populations that experienced similar fish predation pressure. We thus found that a shared selection pressure resulted in a similar allocation of trait change across the ecological, evolutionary, and eco-evolutionary contributions, and this result was independent of the approach used (alternatively one could have used the third spatial modification and calculated average contributions of the two directions of trait change, detailed in Appendix S6). Our analysis thus suggests that in this case adaptation through time and across space is achieved through similar combinations of mechanisms. This also suggests that the spatial differentiation observed in De Meester (1996) could in principle be achieved in a time span of a few years (i.e., the time span of the resurrection ecology study).

DISCUSSION

The phenotypic distribution of spatially separated populations and communities can be structured by nonevolutionary (phenotypic plasticity at the individual level, species sorting at the community level) and evolutionary (genetic differentiation at the population level) processes (Fox & Harder, 2015; Govaert et al., 2016; Kawecki & Ebert, 2004; Logan et al., 2016; Via & Lande, 1985). However, evolutionary and nonevolutionary contributions to trait divergence among populations or communities separated in space cannot always be quantified using the same methods as for population or community trait change in time. Temporal studies may ask how evolutionary and nonevolutionary processes combine to structure trait shifts from one time point to the next (Figure 1a), whereas a spatial study instead seeks to quantify evolutionary and nonevolutionary contributions to among-site trait divergence (Figure 1b). Some spatial studies do assume a direction that allows for identifying an ancestral state, for example, in studies of invasion history (e.g., stickleback colonization of freshwater lakes; Bell et al., 2004; Le Rouzic et al., 2011), range expansions (e.g., Safriel et al., 1994; Swaegers et al., 2014; Volis et al., 2001), and in studies using a space-for-time substitution (Etterson & Shaw, 2001). However, many spatial studies could not reconstruct how traits changed through time or assess changes in community composition resulting from species extinctions and colonizations mediated through evolution (a temporal process). They could, however, quantify the extent to which plasticity, genetic trait differentiation, and species sorting combine to explain among-site differences in trait values.

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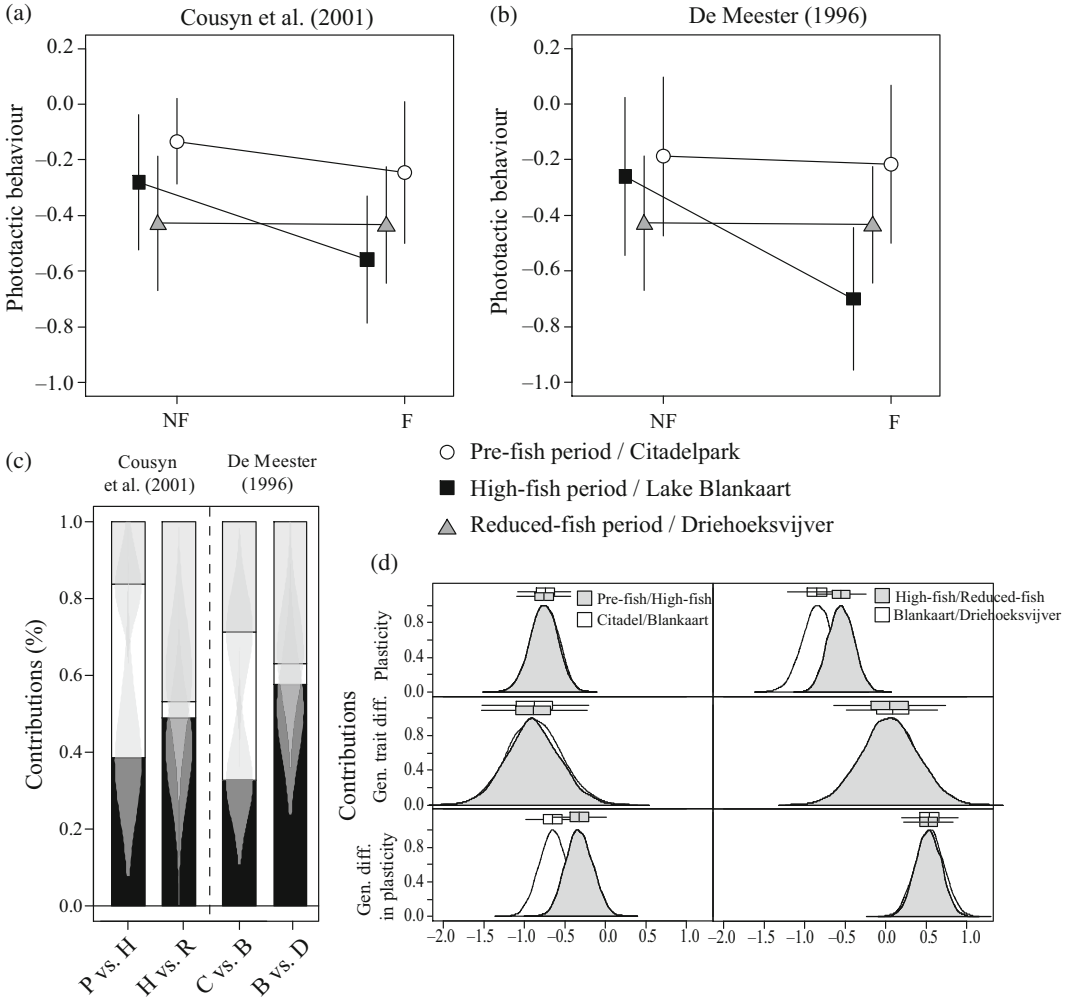

FIGURE 5 Reaction norms of phototactic behavior of three *D. magna* populations originating (a) from the same pond Oud-Heverlee Zuid at three different time periods, corresponding to no (prefish, "P"; circles), high (high fish, "H"; squares), and reduced (Reduced fish, "R"; triangles) fish predation pressure and (b) from three different spatial ponds corresponding to no (Citadelpark, "C"; circles), high (Blankaart, "B"; squares), and low (Driehoeksvijver, "D"; triangles) fish predation pressure measured in a control (NF) and fish kairomone (F) condition (data obtained from fig. 2 in Cousyn et al. (2001) and from fig. 1 in De Meester (1996)). (c) Relative contributions of plasticity (black), genetic trait differentiation (white), and genetic differentiation in plasticity (gray) and their density distribution obtained from bootstrap analysis given as a violin plot within the bars (shaded gray area) to observed difference in phototactic behavior between pairs of time periods: pre-fish ("P") versus high-fish ("H"), and high-fish ("H") versus reduced-fish ("R")—and between pairs of spatial ponds—Citadelpark ("C") versus Lake Blankaart ("B") and Lake Blankaart ("B") versus Driehoeksvijver ("D"). (d) Bootstrap distributions of absolute contributions of plasticity, genetic trait differentiation, and genetic differentiation in plasticity for corresponding time periods (gray) and ponds (white) as described in (C).

Eco-evolutionary partitioning metrics are frequently used to quantify ecological and evolutionary contributions to temporal trait change (Collins & Gardner, 2009; Ellner et al., 2011; Govaert et al., 2016; Price, 1970). In this study, we illustrated three ways to adjust the Price equation (Price, 1970; Price, 1972), the reaction norm approach (Ellner et al., 2011; Govaert et al., 2016), and the PRN equation (Govaert et al., 2016) to match spatial, undirected comparisons of discrete trait shifts. The metrics we focus on partition finite trait differences, which often make them dependent on the choice of reference. We demonstrated that this choice of reference can influence the contribution of ecological and evolutionary processes, resulting in different conclusions on the importance of ecology versus evolution when a different reference is chosen. This dependence on the reference is ultimately a problem when the goal is to partition discrete trait differences in spatial study systems, in which the ancestral state or direction of evolution might be unknown and the reference may have to be chosen based on theory, expertise, or perhaps even arbitrarily. To account for this, we proposed three modifications of

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existing discrete-time metrics to partition spatially undirected trait data. While we here focus on the extension of these metrics to studies on spatial structure, the use of these modified metrics goes beyond this extension. For example, the modified metrics also allow for comparing trait divergence observed in, for instance, experimental treatments. More generally, the metrics for undirected trait shifts can in principle be used in any instance where research questions involve the quantification of ecological and evolutionary contributions to trait shifts where no direction of the trait shift is known or implied. To demonstrate this, we also applied some of the metrics to published case studies of empirical data to illustrate the different questions that can be addressed when the metrics are matched to field or laboratory data.

We presented three options to quantify ecological and evolutionary contributions to spatial trait divergence using existing partitioning metrics. Briefly, the first modification involves constructing a group reference that can represent a known ancestral state, a control treatment, or a calculated group mean and evaluates how local populations differ from that reference. The construction of a common reference allows researchers to associate the calculated ecological and evolutionary contributions to a single treatment effect or to population- or community-specific characteristics. For example, among-population genetic differentiation is expected when subpopulations are spatially isolated (Bohonak, 1999; Wright, 1943). This expectation can then be validated using spatially modified partitioning metrics and comparing the contribution of evolutionary trait shift with the population's degree of spatial isolation.

More specific eco-evolutionary hypotheses, for example whether or not populations with a longer history of exposure to a selection pressure (Ghalambor et al., 2007; Oostra et al., 2018), different selection pressures (Huang & Agrawal, 2016), or with a different degree of environmental variability (Chevin & Hoffmann, 2017; Reed et al., 2010) demonstrate a larger fraction of genetic evolution versus plasticity could be tested by comparing the different fractions to these site properties. For example, a recent study by Govaert et al. (2021) demonstrated spatial variation in the contribution of evolution in a focal zooplankton species *D. magna* for community trait values and showed that this variation was better explained by ecological properties of the zooplankton communities in which the focal species was embedded than by its population genetic properties.

The second and third modifications we presented do not require designating a common reference. They instead use different methods of averaging and consider comparisons between pairs of populations. In the second modification, we presented a version of the metrics for undirected trait shifts by averaging population's trait values and abundances when calculating the ecological and evolutionary components. However, when such modification toward a version for undirected trait shifts is not possible, the last modification can be used. In the current study, this was the case for the reaction norm and PRN approach, but not for the Price equation. In the third modification, one calculates the ecological and evolutionary components of among-population trait differences by treating each population in the pair as the reference, then averaging the two resulting absolute values for each component. Averaging the absolute values of each component means that the resulting ecological and evolutionary contributions will not add up to the observed trait difference. Hence, for this modification only relative contributions are meaningful. This third modification thus produces an overall assessment of how the relative importance of ecological and evolutionary processes varies among a set of spatially separated populations or communities. For the reaction norm approach, the second and third modifications will result in identical relative contributions of ecology and evolution in specific cases (see section *Modification 3*, reaction norm approach).

These spatially modified eco-evolutionary partitioning metrics were applied to data from three existing studies to illustrate how they can answer eco-evolutionary research questions. Spatial partitioning metrics can identify spatial structure in the relative contributions of ecological and evolutionary processes to trait variation in natural landscapes. Spatial variation in abiotic conditions and ecological interactions may result in spatially divergent selection strengths, producing distinct evolutionary trajectories among populations (and between coevolving species, i.e., the geographic mosaic of coevolution) (Thompson, 1999, 2005). These different selection pressures in a heterogeneous landscape might result in varying contributions of ecological and evolutionary processes, and these contributions could further depend on the population or community identity or on the focal species studied. The case study of Urban (2008) indicated that populations of *A. maculatum* living in the presence of the predator *A. opacum* had substantially higher contributions of genetic differentiation in plasticity and showed larger variation in their genetic trait differentiation than populations living in the absence of the predator. The populations living in the absence of the predator showed a strikingly narrow range in the relative contribution of genetic trait differentiation in larval body size. Similarly, the case study of Weider et al. (2008) indicated that eco-evolutionary contributions differed depending on experimental treatments, but also among species, although there are currently no clear expectations for when this dependence is more or less likely. Nevertheless, the indication of context-dependent eco-evolutionary

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processes is important for future research in the field of eco-evolutionary dynamics.

It currently is unknown to what extent the magnitude of eco-evolutionary contributions to population and community trait change is predictable and repeatable. In this study, we used spatial eco-evolutionary partitioning metrics to compare how *D. magna* traits responded to the presence of fish predators and found a similarity in eco-evolutionary responses in phototactic behavior between populations with spatial variation in this selection pressure and populations with temporal variation. Although the similarity in spatial and temporal trait shifts was previously explored for the *D. magna* populations used in this study (Freeman & Herron, 2007), our application explores whether eco-evolutionary contributions to spatial and temporal trait shifts are also repeatable in space and time. This is an intriguing possibility, because it has been hypothesized that trait evolution dynamics in space and time can be similar (e.g., Frank, 1991; Gandon et al., 2008). Our results indicate this similarity may also be reflected when considering both plastic and genetic trait responses to selection pressures. We anticipate that further comparative studies will be needed to establish whether this is a repeatable pattern.

Intraspecific trait variation can be a critical component of population dynamics, community structure, and ecosystem functioning in a wide range of settings (Des Roches et al., 2018; Mimura et al., 2017). However, the importance of intraspecific variation for ecology is likely to vary, and quantifying the drivers of this variation will be important in future research studies. Some important questions remain to be answered next: How much of this intraspecific trait variation is due to genetic trait variation? To what extent does the ecological importance of genetic trait variation differ across landscape properties such as connectivity, across biotic and abiotic environmental gradients, and in response to interactions with other species? The approaches outlined here to adapt existing eco-evolutionary partitioning metrics to appropriately accommodate spatially structured (undirected) trait data will facilitate future attempts to determine associations between among-site variation in ecological and evolutionary components and properties of the landscape, the environment, or the study species. Numerous studies compare trait distributions among communities (Cornwell & Ackerly, 2009; Kenitz et al., 2018; Vellend, 2016) or population genetic structure among populations (Ackerman et al., 2013; Gomez-Uchida et al., 2009; Marten et al., 2006; Olsen et al., 2011; Short & Caterino, 2009). However, very few studies collected the necessary data to decompose all potential sources of trait shifts at the community level. We anticipate an increase in the number of studies that attempt to combine surveys of genetic and nongenetic trait variation at the population level with species composition and associated trait shifts at the community level (e.g., Govaert et al., 2021). The data gathered by such studies can be used to quantify the contributions of evolutionary and nonevolutionary processes to among-site variation in community trait values, quantifying the structure of the evolving metacommunity. We therefore predict an increasing scope for the application of the metrics proposed in this study.

AUTHOR CONTRIBUTIONS

All authors together developed the ideas and approaches for the study. Lynn Govaert performed mathematical calculations and data analysis with input from Jelena H. Pantel and Luc De Meester. Lynn Govaert wrote a first draft of the manuscript with input from Jelena H. Pantel and Luc De Meester. All authors contributed to subsequent revisions of the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Govaert et al., 2022a) are available on Dryad at https://doi.org/10.5061/dryad.0vt4b8gz8. Code to perform the data analysis and construct the figures (Govaert et al., 2022b) is available on Zenodo at https://doi.org/10.5281/zenodo.4600596.

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