Title: Coexistence of phenotypic plasticity and habitat use in natural populations

Samantha C. Patrick[1*], Julien Martin[2], Anne Charmantier[3], Laura Gervais[3,4], Pierre-Olivier Montiglio[5], and Denis Réale[5]

Affiliations

1. University of Liverpool, Earth, Ocean and Ecological Sciences, School of Environmental Sciences, Liverpool, Merseyside, UK L69 3BX; samantha.patrick@liverpool.ac.uk; +44 151 7954390 *corresponding author
2. University of Ottawa, Ottawa, ON, CA; julien.martin@uottawa.ca
3. Centre d'Ecologie Fonctionnelle et Evolutive, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France; anne.charmantier@cefe.cnrs.fr
4. Université de Toulouse, INRAE, CEFS, Castanet-Tolosan, France and LTSER ZA PYRénées GARonne, Auzeville-Tolosane, France; laura.gervais@inrae.fr
5. Université du Québec à Montréal, Sciences Biologiques, 141 Président-Kennedy, Montreal, QC, CA H3C 3P8; montiglio.pierre-olivier@uqam.ca; reale.denis@uqam.ca

Open research statement: There is no data in this paper but code for simulations can be found here: DOI: 10.17605/OSF.IO/N95WS and Github: https://github.com/JulienGAMartin/phenotype_oikotype_covariation with further details available in supplementary material appendix 2

Keywords - Phenotypic plasticity, matching habitat choice, habitat use, niche construction, double hierarchical models, extended phenotype, NC^3, adaptation to environmental change

Abstract

When studying how individuals adapt to environmental changes, the environment is traditionally viewed as a passive backdrop, with individuals modifying their phenotype in response to environmental conditions (i.e., phenotypic plasticity). However, this perspective overlooks the active role of habitat choice in mediating individual responses to environmental changes. In this paper, we argue for the explicit inclusion of habitat use as an individual metric, which we term the 'oikotype', and explore its implications for understanding individual–environment interactions. We propose a conceptual framework that focuses on the patterns of among- and within-individual (co)variation between phenotype and oikotype, offering new insights into the processes that shape adaptation to changing environments. We complement this framework with a description and discussion of appropriate statistical approaches and outline how it can be extended to incorporate niche construction. Ultimately, integrating phenotypic plasticity, habitat use, and habitat modifications into a unified model is essential for understanding how organisms make decisions and adapt to a changing environment.

1. Introduction

Habitat is an essential dimension of the ecology and evolution of living organisms (Davis 1960; Davis & Stamps 2004; Johnson 2007; McComb 2007) as it influences the survival, reproduction, and fitness of individuals, thereby shaping population dynamics, community structures, and ecosystem functions. Its degradation, fragmentation, or destruction represent some main causes of the recent biodiversity crisis of the Anthropocene (IPBES 2019).

Habitat is traditionally studied as an external driver of phenotypic variation, outside the individual's control; it represents selection pressures that the individual organisms undergo.

This vision of habitat, as a selective agent only, however, omits important interactions between an organism and the abiotic and biotic (including social) components of its immediate environment. For example, an organism can change its phenotype according to its environment (i.e., phenotypic plasticity or niche conformance), move to experience different environmental conditions (i.e., non-random use of available habitat sets, habitat or niche use), or even modify its environment (i.e., niche construction), all these actions leading to different fitness benefits and costs (Edelaar & Bolnick 2019; Takola & Schielzeth 2022; Trappes *et al.* 2022). Omitting these interactions may lead to incomplete assumptions when studying the factors that reduce or maintain phenotypic and genetic variation within or between populations.

Among such processes available, individuals can change their phenotype in response to ecological conditions they experience (Edelaar & Bolnick 2019; Turko & Rossi 2022) Individuals or genotypes differ in their ability to show phenotypic plasticity in response to the environment (Araya-Ajoy & Dingemanse 2017; Brommer *et al.* 2005; De Jong 2005; Lande 2009; Pfennig 2021). Such genetic or individual variance for plasticity finds its explanation in the cost of the machinery used by the organism to adjust to the environment or potential errors associated with the uncertainty of the cues (DeWitt 1998; DeWitt *et al.* 1998). Because phenotypic plasticity offers a way for the individual to extend the range of environmental conditions it can live in, and individuals differ in their plasticity, this process can explain why individuals do not use the same subsamples of environmental conditions in their habitat, generating phenotype-environment correlation (e.g., bigger individuals occupy richer habitats). However, studies fail to consider the role of habitat choice in the maintenance of variation in plasticity within populations.

Animals can also actively choose habitats based on their features (Hamilton 2017; Mayor *et al.* 2009; Montgomery & Roloff 2013; Rosenzweig 1991). Habitat choice involves the preference of the individual (i.e., the likelihood that an animal selects an item when offered uses on an equal basis (Johnson 2007). Animals may choose a restricted range of habitat features among the ones available because they show higher fitness when using these values compared to others. Several proximate mechanisms can drive the variation among conspecifics in the habitat chosen. First, habitat choice may depend on genetic variation in habitat preference (Akcali & Porter 2017; Jaenike & Holt 1991; Wecker 1964). Second, the natal habitat preference induction hypothesis predicts that individuals should choose a habitat with similar features to their natal habitat because their parents have succeeded in that habitat (Stamps & Davis 2006). Third, the matching habitat choice hypothesis predicts that animals choose to use the habitat in which they perform the best based on their phenotype, beyond their age, sex, dominance rank, or state (Akcali & Porter 2017; Edelaar *et al.* 2008; Munar-Delgado *et al.* 2024). All the above mechanisms are not mutually exclusive and can lead to a strong correlation between the phenotype, genotype, and the environment (Saltz & Nuzhdin 2014), making it difficult to distinguish among them.

A third alternative process is an organism's ability to alter habitat, or niche construction, in a way that improves that organism's fitness (Laland *et al.* 2015; Lewontin 1983). While some very well-known examples of niche construction include beaver dams, coral reefs and termite mounds, many organisms do alter their habitat to some extent (e.g., burrow systems, nests, food caches, host manipulation by a parasite). However, just as organisms are able to combine habitat choice and plastic response to this habitat, they may both be able to alter their habitat and adjust their phenotype to their habitat (altered or not), and the degree of habitat alterations may vary among individuals (Trappes *et al.* 2022).

Plasticity, habitat choice, and niche construction have been the subject of numerous theoretical and empirical studies, although they have traditionally been studied separately. For the moment, however, we still know little about the coexistence or coevolution of these different processes, within and among individuals and populations as well as the respective role of each in constraining or facilitating the evolution or the development of other processes. In the last decade, several authors have investigated the interaction between phenotypic plasticity and matching habitat choice, and which strategy might be the most beneficial in terms of fitness. Edelaar *et al.* (2017) assessed whether plasticity *versus* matching-habitat choice evolves depending on the degree of temporal variation in the environment, the costs of multiple underlying traits, the order of dispersal, and development of traits. In a subsequent simulation study, Nicolaus and Edelaar (2018) showed a greater adaptive potential for matching habitat choice compared to plasticity, and that matching habitat choice is better at preventing local maladaptation (Scheiner 2016). Many empirical studies to date come from spatial ecology and tracking data. Animal migration usually occurs so animals can find optimal habitats such as mammals following the 'green wave' to optimise their habitat and resource acquisition (Merkle *et al.* 2016). The movement of animals during migration can also change the habitat itself (Geremia *et al.* 2019) and individuals may face a trade-off between plastic changes in behaviour and finding the optimal habitat (Shoji *et al.* 2014; Warwick-Evans *et al.* 2016). Beyond this field, in their empirical study on dunnocks, Holtman *et al.* (2017) showed that bold individuals settled in areas with high human disturbance, that birds became bolder with age, and that habitat choice had a larger influence on phenotypic distribution than plasticity. Lowe and Addis (2019) found that both phenotypic plasticity and matching habitat choice occurred in salamanders with individual level differences in their importance. Finally, Turko and Rossi (2022) found that habitat choice

accentuated metabolic plasticity in both fish and frog species, demonstrating the importance of considering both processes.

Despite some theoretical and empirical work, there are still gaps in our knowledge of the relative combined contribution of habitat choice, niche construction, and plasticity in explaining phenotypic differentiation within and across populations. While the idea that habitat choice and phenotypic plasticity can evolve under different spatiotemporal environmental conditions has been discussed and investigated at the population level (Edelaar *et al.* 2008; Jacob *et al.* 2015; Webber *et al.* 2023), we need a framework for within-population individual level differences in habitat choice, niche construction and phenotype plasticity, and the development of suitable modelling techniques. For example, Edelaar *et al.*'s (2008) matching habitat choice conception focuses mainly on the first stage of life when individuals disperse from their natal area to settle in a new habitat. Habitat choice, however, can occur at many different spatiotemporal scales, from micro-site selection daily at a small spatial scale when foraging, to dispersal and settlement in a habitat at a larger spatial scale (Mayor *et al.* 2009). While the framework proposed by Edelaar and Bolnick (2019) or by Turko and Rossi (2022) sets out the importance of individual level differences, addressing these multiple scales of analysis poses methodological challenges. Furthermore, in the past, there has been a focus on habitat choice and selection but these differ from habitat use. An individual can have a strong preference for a habitat, but that habitat may not be available to them (Lele *et al.* 2013) or they may be forced to use a habitat through a range of processes not aligned with the individual's choice. While habitat selection and choice can be seen as mechanisms driving habitat use, it is the used habitat that will ultimately affect an individual's fitness, making this distinction critical. We tackle here the timely task of modelling the interactions between plasticity and habitat use (and, by extension, niche construction) at

different hierarchical levels of life and explore how these strategies have coevolved and kept coevolving.

We present a statistical approach to study the patterns of variance and covariance between one or more phenotypic traits of an individual and one or more features of its immediate environment to infer the coexistence between phenotypic plasticity and habitat use. While our paper focuses more heavily on habitat use and its outcomes, rather than its alteration by the organism (niche construction), the principles and models can be applied to both processes. Furthermore, the proposed approach could help estimate the fitness consequences of combinations of an individual's habitat features and phenotypes, to help us test assumptions regarding their coevolution. Our proposed method should help conceptualise the possible coexistence of phenotypic plasticity, habitat use, or niche construction as possible alternative strategies within a population and encourage more theoretical work to generate hypotheses about the underlying processes leading to their coexistence.

2. Conceptual similarities and differences between an individual's traits and the features of its habitat

We first need an operational definition of habitat that is appropriate for our objectives. Despite its profound eco-evolutionary significance, the ways of conceptualising the habitat are numerous and have evolved over time without scientific consensus in evolutionary ecology. This leads to imprecision and ambiguity in what researchers mean by the term habitat (Block & Brennan 1993; Whittaker *et al.* 1973). First, the interchangeable use of the terms environment and habitat has led to confusion in differentiating them (Davis 1960) alongside a lack of consensus of what habitat really means. Perhaps one of the broadest definitions is given by Matthiopoulos *et al*. (2023), who define habitat as *"a point in*

176 *environmental space whose dimensions are resources, risks, and conditions".* This is
177 definition of habitat allows the inclusions of conditions where animals are not found. Another
178 popular definition comes from, Hall *et al*. 1997 . as: *"the resources and conditions present in*
179 *an area that produce occupancy — including survival and reproduction — by a given*
180 *organism."* However, including fitness benefits in the definition prohibits the study of
181 maladaptive habitats, which are important to consider. We also clarify the levels at which
182 occupancy and use can occur, which allows us to focus on quantifying among- or within-
183 population variation in habitat use and integrate processes that can explain the non-random
184 distribution of individuals of a species or population within their general habitat. Throughout
185 this article, we build on previous definitions cited above and consider that a habitat is *a set of*
186 *spatial points in time, used by a species, a population, or an individual, each of them*
187 *characterized by a set of abiotic and biotic features.*
188
189 We define a trait as "*a characteristic of an organism shared by all or some individuals of ae-*
190 *cies that can vary, although not necessarily, among these individuals*" (Réale *et al.* 2007).
191 The phenotype is a measure of that trait. Some traits can evolve, although they are not directly
192 measured on the organism. For instance, house mice (*Mus musculus*) show heritable differ-
193 ences in the mass of cotton used to build their nest (Lynch 1980). Dawkins (1982) proposed
194 to use the term extended phenotype to describe these traits. He defined them as *"the pheno-*
195 *type of an organism…"* that *"…extends beyond its body to encompass the organism's behav-*
196 *ior and the consequences of that behavior."* While mostly applied to physical structures, such
197 as beaver dams and nests in birds, if an individual has control over their habitat, habitat can be
198 considered as an extended phenotype in a much broader sense (Edelaar & Bolnick 2019).
199 With this definition in mind, we can consider that a feature of the habitat in which we find an
200 individual is one of its "traits". While encompassed in the broad phenotype of an individual,

this extended phenotype is differentiated from phenotypic traits measured on an individual, as it is measured on an external feature, in this case habitat.

The breadth of traits, which can be considered as an extended phenotype, has yet to be fully explored, but as we focus very specifically on habitat in this paper, we propose to name "oikotype" (Greek *oikos* = house and *typos* = mark) as the measure of a feature of the habitat used by an individual/genotype (hereafter an individual). This feature can be abiotic (e.g. temperature), or biotic (e.g. vegetation cover, density of conspecifics). Oikotypic distribution can either be continuous (e.g., temperature gradient, population density, sex ratio), or discrete and categorical (e.g., type of forest). Oikotypes for a habitat feature can display continuous spatiotemporal variation or show more heterogeneous, fine-grained to coarse-grained, spatial and temporal distributions, interspersed with other oikotypes. As a population shows a phenotypic mean and variance for a trait, this population can show an oikotypic mean and variance for a feature of a habitat in which it lives (Figure 1). Individuals within a population can differ in their oikotypic mean and variance (e.g. their oikotypic mean can deviate from the population oikotypic mean), which define their differences in niche specialisation (level and width). To employ semantics commonly used in quantitative genetics, the phenotypic variance is the variance of all measures of a trait in a population (Falconer & Mackay 1996). By extension the oikotypic variance is thus the variance of all the measures of the habitat feature in a population, including preference and availability.

The phenotypic variance of a trait or the oikotypic variance of a habitat feature, and their covariance can be decomposed into (co)variances at different hierarchical levels (Figure 1). First, we may find variance among individuals in their mean trait and mean habitat feature (different positions of the individual along the x- and y-axis Figure 1). This among-individual

variance can be attributed to genetic differences between individuals if phenotypes and oikotypes are heritable. Individuals then differ consistently in the value of the trait (e.g., body mass) or of the feature of the habitat they use (e.g., density of trees). The trait and the habitat feature can vary independently of each other (Figure 1a), but they can also covary, both among individuals (correlation across ellipses in Figure 1b) and within individuals (differences in the shape of ellipses, see next paragraph). A positive or a negative covariance among individuals means that one can predict the phenotype of an individual based on the feature of the habitat it uses, and vice versa.

The second level of decomposition of the phenotypic and oikotypic (co)variance occurs within individuals (different sizes and shapes of ellipses in Figure 1). Within-individual (co)variance can be attributed to plastic changes in the trait and to changes in the use of the habitat occurring during the study period. Within-individual variance in a habitat feature relative to the variance among individuals reflects the degree of individual specialisation for that feature: Generalists show a high within-individual variance in their habitat feature (darker blue ellipses), whereas specialists show a restricted variance (lighter blue ellipses). Differences in within-individual variance in a habitat feature may not reflect different active uses by individuals for a restricted *versus* a more variable range of environmental conditions but may instead reflect constraints on what each individual can use. For example, an individual may be socially constrained in its variation for a habitat feature. We, therefore, should not assume the adaptive nature of an individual oikotype mean or variance, just as within-individual variation in phenotypic traits may not always be adaptive. Note that whether a phenotypic or oikotypic trait value is adaptive relative to the population's mean value for that trait can be tested, for example, by assessing its average relative fitness.

3. The phenotype-oikotype coevolution

Evolution of preference for a specific range of values of a habitat feature (oikotypic mean and variance) would occur if the population improves its average fitness in that range of habitats compared to other habitats (Edelaar *et al.* 2008). Furthermore, as for the evolution of traits within populations, one condition for the evolution of habitat use is that individual oikotypic variation has a genetic basis. The evolution of habitat use requires individuals to have the ability to perceive and have access to habitats and select based on their features.

Within the range of oikotypes of a population, all individuals may not show equal fitness, and thus individuals may use a restricted range of the habitat features used by their population (e.g., individual niche specialisation; Bolnick *et al.* 2003). Studying the phenotype and the oikotype jointly may help us understand which mechanisms are important in the maintenance of variance in plasticity and habitat use within natural populations. Correlational, or context dependent, selection favouring different combinations of phenotypes and oikotypes may lead to the coevolution between an organism's trait and habitat use (Dingemanse & Réale 2022), such that an individual's phenotype matches its oikotype. The variation in phenotypes or oikotypes could, thus, be maintained if each phenotype shows higher fitness in a unique, restricted range of oikotypes. Correlational selection should lead to some genotype-environment covariance or phenotype-environment covariance. Individuals use a restricted range of the oikotypic variance of the population because they differ in their genotypes or built-up different phenotypes early in life. It is therefore necessary to conceptualise the possible coexistence between plasticity, habitat use or construction that may lead to adaptive match between phenotypes and oikotypes. Another alternative, is the coexistence of plastic individuals with weak habitat preferences (or scope for habitat use) and non-plastic individuals with stronger habitat preferences. The presence of a coevolution between

phenotypic plasticity and habitat use might predict differences in plasticity or in the strength of preferences for particular habitat within population to be pervasive.

In this section we present statistical models decomposing (co)variation in phenotypes and oikotypes, and assess the relative importance of the variation in shaping this covariance. These models require repeated and (ideally) simultaneous measures of an individual's phenotype and oikotype for the trait(s) and habitat features of interest, respectively. This will be more difficult for traits that are fixed very early in life. Alternatively, using genetic relatedness information, we could run an animal model to estimate the genetic and residual (co)variance between the trait and the habitat feature. In this case, one record of phenotype and associated oikotype per individual might be sufficient, if we assume a single measurement is representative of the individual average, but multiple recordings per genotype would be ideal (Jablonszky & Garamszegi 2024). Although, in principle, including genetic relatedness information into these model structures is feasible, we here focus on the decomposition of the among and within-individual covariance.

The first step in the analyses of the links between phenotypes and oikotypes is to use a multivariate generalised linear mixed model (MGLMM; note that these models are also called multivariate hierarchical generalised models). A guide to the different modelling types we use in this paper can be found in Supplementary material Appendix 1. MGLMM builds on a GLMM (Figure 3a) and estimates the among- and within-individual variances in both the phenotype and the oikotype, and their among- and within-individual covariances (Figure 3b). This model is the least complex and the one requiring the smallest amount of information. In this model, at least one trait (y) and one habitat feature (h) are analysed together (also called a bivariate model), following these generalised linear mixed models:

$$y_{ij} = \sum_k \beta_k X_{k_{ij}} + \alpha_{y,m_i} + e_{y_{ij}} \quad \text{Equation (1a)}$$

$$h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h,m_i} + e_{h_{ij}} \quad \text{Equation (1b)}$$

Where y_{ij} and h_{ij} are the phenotypic and oikotypic measures of individual i at instance j, β_k and β_n are the coefficients of fixed effects $X_k$and X_n, respectively, $\alpha_{y,m_i}$and $\alpha_{h,m_i}$are the individual deviations from the mean for the trait y and habitat feature h, and $e_{y_{ij}}$ and $e_{h_{ij}}$ are the residuals for the phenotype of trait y and the oikotype of habitat feature h. The individual random effects are assumed to follow a multivariate normal distribution with means 0 and a variance matrix Σ_{id} to be estimated.

$$\begin{bmatrix}\alpha_y \\ \alpha_h\end{bmatrix} \sim N_2\left(0, \Sigma_{id} = \begin{bmatrix}\sigma^2_{id_y} & cov(id_y, id_h) \\ cov(id_y, id_h) & \sigma^2_{id_h}\end{bmatrix}\right) \quad \text{Equation (2)}$$

Similarly, the residuals for both traits are assumed to follow a multivariate normal distribution with means of zero and a variance matrix Σ_e to be estimated.

$$\begin{bmatrix}e_y \\ e_h\end{bmatrix} \sim N_2\left(0, \Sigma_e = \begin{bmatrix}\sigma^2_{e_y} & cov(e_y, e_h) \\ cov(e_y, e_h) & \sigma^2_{e_h}\end{bmatrix}\right) \quad \text{Equation (3)}$$

The two estimated variance components (i.e., $\sigma^2_{id_y}$ and $\sigma^2_{id_h}$) indicate whether individuals differ consistently in the values of the phenotype and of the oikotype measured. For example, in Figure 1, we will estimate the among-individual variance in body mass and in the density of trees in the plot.

The among-individual covariance, $cov(id_y, id_h)$ equation 2 shows whether the average individual phenotype for the trait increases or decreases with its average oikotype for the habitat feature. In Figure 1, that covariance will be positive and will indicate that an individual's average body mass increases with its density of trees in the plot.

The within-individual (residual) covariance $cov(e_y, e_h)$ equation 3, between the trait and the

habitat feature, measures the global individual adjustment of their phenotype in response to changes in their oikotype, or vice versa. For example, in Figure 1, a positive covariance within individuals will indicate that when the bird is moving to a plot with denser trees, it also increases its mass. The residual covariance is assumed to be the same for all individuals and could also include combined measurement errors in the trait and the habitat feature and/or covariation of the trait and oikotype with unmeasured variables. Thus, the residual covariance could be an overestimation or underestimation of the individual adjustment of the trait in response to changes in the habitat feature. For visualisation see Figure 3b.

An extension of this model could be to use a multivariate double-hierarchical generalised linear mixed models (MDHGLM). This model is an extension of the MGLMM (Figure 3b) that removes the assumption that the residual variance is identical to all individuals and instead directly estimates among-individual variation in residual variance (O'Dea *et al.* 2022). It also builds on a DGHLM where the residual variance is modelled in the trait but not the habitat (Figure 3c). To do so, the model considers that the residuals for each observation for each individual come from a normal distribution with a mean of zero and a residual variance specific to that observation. The observation-specific residual variance can then be modelled using a hierarchical structure combining both fixed and random effects on the residual variance. This model is a multivariate version of DHGLM (Cleasby *et al.* 2015; Lee & Nelder 2006; O'Dea *et al.* 2022). Building on equations 1a, 1b and 2, the MDHGLM can be written as:

$$y_{ij} = \sum_k \beta_k X_{k_{ij}} + \alpha_{y,m_i} + e_{y_{ij}} \text{ and } ln\left(\sigma_{e_{y_{ij}}}\right) = \sum_l \gamma_l X_{l_{ij}} + \alpha_{y,v_i} \quad \text{Equation (4a)}$$

$$h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h,m_i} + e_{h_{ij}} \text{ and } ln\left(\sigma_{e_{h_{ij}}}\right) = \sum_o \gamma_o X_{o_{ij}} + \alpha_{h,v_i} \quad \text{Equation (4b)}$$

where γ_l and γ_o are the coefficients of fixed effects for the within-individual residual variance X_l and X_o, respectively. α_{y,m_i}, α_{h,m_i}, α_{y,v_i} and α_{h,v_i} are the individual deviations from the mean

(subscript *m*) and within-individual variance (subscript *v*) for the trait *y* and habitat feature *h*. The individual random effects, α, are assumed to follow a multivariate normal distribution with means 0 and a variance matrix Σ_{id} to be estimated.

$$\begin{bmatrix}\alpha_{y,m}\\ \alpha_{y,v}\\ \alpha_{h,m}\\ \alpha_{h,v}\end{bmatrix} \sim N_4\left(0, \Sigma_{id} = \begin{bmatrix}\sigma^2_{id_{y,m}} & . & . & .\\ cov(id_{y,m}, id_{y,v}) & \sigma^2_{id_{y,v}} & . & .\\ cov(id_{y,m}, id_{h,m}) & cov(id_{y,v}, id_{h,m}) & \sigma^2_{id_{h,m}} & .\\ cov(id_{y,m}, id_{h,v}) & cov(id_{y,v}, id_{h,v}) & cov(id_{h,m}, id_{h,v}) & \sigma^2_{id_{h,v}}\end{bmatrix}\right)$$

Equation (5)

Colour blocks in the matrix regroup parameters from the phenotypic model in pink, the oikotypic model in yellow and the covariance between the phenotype and the oikotype in orange.

The residuals are also assumed to follow a multivariate normal distribution with means of zero and a variance matrix Σ_e to be estimated.

$$\begin{bmatrix}e_y\\ e_h\end{bmatrix} \sim N_2\left(0, \Sigma_e = \begin{bmatrix}\sigma^2_{e_y} & cov(e_y, e_h)\\ cov(e_y, e_h) & \sigma^2_{e_h}\end{bmatrix}\right) \qquad \text{Equation (6)}$$

Note that when specified like in equation 6 (the default specification in most software including brms (Bürkner 2017) and ASReml (Gilmour *et al.* 1995)), the residual covariance/correlation estimated will include covariation due to shared fixed effects on the residual variance as well as covariation due to shared measurement error, and due to plasticity in the trait with changing oikotype. For visualisation see Figure 3d.

The advantage of the MDHGLM over MGLMM is that it cannot only test for the hypothesis that the population is, on average, composed of non-plastic specialists *versus* plastic specialists, but can also estimate variation in specialisation in both the trait and the habitat feature among individuals and their correlation (see below in Figure 4). MDHGLM cannot explicitly test for either the phenotypic plasticity of the trait in response to the habitat feature,

or the among-individual variation in plasticity of the trait. This is caused by the fact that within-individual residual covariance estimated includes covariation due to multiple sources, including phenotypic plasticity, associated measurement errors and individual level micro-environmental variation, for example. Thus, the residual covariance can strongly under or overestimate the plasticity.

As an additional extension, we propose the causal structure mixed models (CSMM). The CSMMs are similar to recursive models (RM) in quantitative genetic (Gianola & Sorensen 2004; Varona & González-Recio 2023) as both modelling approaches take into account the causal relationship among traits but CSMMs do not routinely estimate genetic variation (but can easily be extended to do so). The main difference between the previous multivariate models and the causal structure model is that the latter can explicitly fit and estimate plasticity in response to variation in the oikotype and estimate the among-individual variation in phenotypic plasticity. Inversely, if the causal assumption is that the oikotype is changing as a function of the phenotype, this can also be fitted. However, we focus here on the impact of the oikotype on the phenotype. The causal structure model can be fitted either with GLMMs or with DHGLMs, thereby estimating the among-individual variation in within-individual variance or the variation in specialisation in one or both traits. Here we describe the most complex causal structure model using DHGLMs for phenotypes and oikotypes simultaneously (See Figure 3).

In this model, we explicitly fit a plastic response to the oikotype in the trait model with a random slope for oikotype at the individual level, and at the same time we estimate the model of the oikotype. Building on the DHGLM equations, the model can be written as:

$y_{ij} = \sum_k \beta_k X_{k_{ij}} + (\beta_h + \alpha_{y,p_i}) h_{ij} + \alpha_{y,m_i} + e_{y_{ij}}$ and

$$ln\left(\sigma_{e_{y_{ij}}}\right) = \sum_l \gamma_l X_{l_{ij}} + \alpha_{y,v_i}$$ Equation (7a)

$$h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h,m_i} + e_{h_{ij}} \text{ and } ln\left(\sigma_{e_{h_{ij}}}\right) = \sum_o \gamma_o X_{o_{ij}} + \alpha_{h,v_i}$$ Equation (4b)

where β_h is the average plasticity slope of the changes in the trait as a function of the oikotype h. α_{y,p_i} is the individual deviation from the average plastic response as a function of the oikotype. The random effects, α, are assumed to follow a multivariate normal distribution with means 0 and a variance matrix Σ_{id} to be estimated.

$$\begin{bmatrix} \alpha_{y,m} \\ \alpha_{y,p} \\ \alpha_{y,v} \\ \alpha_{h,m} \\ \alpha_{h,v} \end{bmatrix} \sim N_5 \left(0, \Sigma_{id} = \right.$$

$$\left. \begin{bmatrix} \sigma^2_{id_{y,m}} & . & . & . & . \\ cov(id_{y,m}, id_{y,p}) & \sigma^2_{id_{y,p}} & . & . & . \\ cov(id_{y,m}, id_{y,v}) & cov(id_{y,p}, id_{y,v}) & \sigma^2_{id_{y,v}} & . & . \\ cov(id_{y,m}, id_{h,m}) & cov(id_{y,p}, id_{h,m}) & cov(id_{y,v}, id_{h,m}) & \sigma^2_{id_{h,m}} & . \\ cov(id_{y,m}, id_{h,v}) & cov(id_{y,p}, id_{y,v}) & cov(id_{y,v}, id_{h,v}) & cov(id_{h,m}, id_{h,v}) & \sigma^2_{id_{h,v}} \end{bmatrix} \right)$$ Equation (8)

As in equation 5, colour blocks in the matrix regroup parameters from the phenotypic model in pink, the oikotypic model in yellow and the covariance between the phenotype and the oikotype in orange.

Note that the alternative of fitting the oikotype change in response to changes in the phenotype of a trait is also feasible. For example, organisms may change habitat after experiencing important phenotypic changes during their lifetime. Note that with the suggested causal structure, it is not possible to test statistically if the phenotype changes in response to the oikotype or if the oikotype changes as a function of the phenotype, or both, but assumptions about the causal relations should be done to fit the model. In addition, if the data

is available, it would be possible to fit a more complex causal structure allowing to test for the directionality of the causal relation or separate co-occurring effects of habitat use and niche construction. For visualisation see Figure 3.

4. Case study: The infamously aggressive selkie

We include a case study to show the use of these models looking at the interaction between aggression and temperature in wild selkies. Here we simulate data and present the full model output from a CS-DHGLM and the biological interpretation. Full code is archived on OSF (https://osf.io/n95ws/ ; DOI: 10.17605/OSF.IO/N95WS and github (https://github.com/JulienGAMartin/phenotype_oikotype_covariation) and further details can be found in Supplementary material Appendix 2.

Here we show a virtual illustration of how to run the proposed models. Selkies are mythological shape-shifting creatures living along the shores of Scotland. They can take on the form of a seal to exploit the resource rich marine environment. With their seal skin they can move long distances easily and so can cover a vast area. In the focal simulated population, any habitat is available to any individual without limitation. Therefore, habitat preference maps directly onto habitat use. In populations where this is not the case, researchers should consider including habitat availability in the analysis (see section 5 and 6). Selkies can be very aggressive, and there is sexual size dimorphism whereby females are smaller and slenderer than males.

This study aims to answer the following questions:

Q1. Are there among-individual differences in the mean and variance of individual phenotype

441 (aggressiveness) and oikotype (experienced water temperature)?

442 Q2 Do individuals differ in how they change their phenotype in response to the temperature –

443 *i.e.* is there temperature-related plasticity in aggressiveness?

444 Q3 Is there evidence of a covariation between phenotype and oikotype?

445 Q4 Are patterns described in Q1 to Q3 sex-specific?

446

447 Based on a rare data set of 50 selkies (25 males and 25 females) each with 10 observations

448 with measures of aggressiveness and water temperature in the wild. We fitted a causal

449 DHGLM (equations 7a,b) where aggressiveness and water temperature (hereafter

450 temperature) were the trait and habitat feature respectively. The mean part of the model of

451 aggressiveness included sex and temperature as fixed effects and random intercept and a slope

452 with temperature estimated at the individual level. The dispersion part of the model of

453 aggressiveness included sex as a fixed effect and individual identity as a random effect. Sex

454 was included as a fixed effect in both the mean and dispersion part of the aggressiveness

455 model to take into account the sexual dimorphism. Water temperature was also modelled

456 using a DHGLM that included no fixed effect, and only individual identity as a random effect

457 in both the mean and dispersion part of the model.

458

459 This means that the general equations 7a and 4b of the CSMM in this specific case are:

460 $y_{ij} = \beta_{y0} + \beta_X X_{ij} + (\beta_h + \alpha_{y,p_i}) h_{ij} + \alpha_{y,m_i} + e_{y_{ij}}$ and $ln\left(\sigma_{e_{y_{ij}}}\right) = \gamma_{y0} + \gamma_X X_{ij} + \alpha_{y,v_i}$ Equation

461 (10a)

462 $h_{ij} = \beta_{h0} + \alpha_{h,m_i} + e_{h_{ij}}$ and $ln\left(\sigma_{e_{h_{ij}}}\right) = \gamma_{h0} + \alpha_{h,v_i}$ Equation (10b)

463 where in this case *y* and *h* are aggressiveness and water temperature respectively measured

464 repeatedly at the individual level. β_{y0}/ β_{h0} and γ_{y0} / γ_{h0} are the mean value and mean within

465 individual variance in aggressiveness (subscript y) and water temperature (subscript h). X is

sex and β_X and$\gamma_X$are the differences between male and female in mean aggressiveness and within individual variance in aggressiveness. β_h is the plasticity in aggression in response to water temperature for the average individual. $\alpha_{y,m}$, $\alpha_{y,p}$, and $\alpha_{y,v}$, are the individual level deviations (random effects) for mean, slope and variance in aggressiveness while α_{y,m_i} and α_{h,m_i} are the individual level deviations for the mean and variance in temperature.

All results can be found in table 1. We found that female selkies were more aggressive (Median 0.389, HPDI [0.06-0.708]) and more variable in aggressiveness (0.367 [0.106-0.620]) than males. Models revealed among-individual differences in mean aggressiveness (0.207 [0.100-0.379]) and substantial variation in aggressiveness (0.209 [0.115-0.336]. There were among individual differences in the strength of the relationship between aggressiveness and temperature (*i.e.* individual differences in reaction norms; 0.95 [0.025-0.195]). Note that mean temperature differed among individuals (0.220 [0.116-0.363]) but not variation in temperature (0.003 [0.000-0.019]).

When testing for a correlation among strategies, more aggressive selkies were more plastic to temperature (0.667 (0.274-0.943)). More aggressive selkies were found in warmer temperatures (0.693 (0.375-0.954)) as were more plastic selkies (0.473 (0.046-0.827)) and they were more variable in their aggressiveness at a given temperature. More aggressive selkies were less variable in their aggressiveness (-0.512 (-0.803- -0.103)) and selkies with more variable aggressiveness were found in cooler waters (-0.618 (-0.855- -0.3187)).

Overall, these analyses reveal important within- and among-individual variation in selkies aggressiveness. Individuals differed in their average habitat but not in how variable their habitat is, suggesting no evidence of specialist *versus* generalist habitat use in this population.

More aggressive individuals may do better under climate change as they use warmer waters and are more plastic in response to changes to temperature, and these individuals are more likely to be female. This latter result suggests that selkie populations may become more aggressive over time, potentially increasing the risk of human-selkie conflict at-sea.

5. Interpreting patterns of covariation between the trait and the habitat feature

In Figure 4 we show how to use the information from the matrix of variance-covariance obtained from the previous models to infer relations between a trait and a habitat feature at the different hierarchical levels. These scenarios are far from representing all the possible relations between the trait and the habitat feature, and any future empirical study on the subject will have to analyse the matrix precisely to infer these relations.

Figure 4a illustrates a situation where non-plastic individuals with contrasted phenotypes also use distinct but very narrow ranges of oikotypes. In this scenario, we should observe high among-individual variance in *y* and *h*, and covariance between them (MGLMM; $\sigma^2_{id_y}$ and $\sigma^2_{id_h}$ are large and $cov(id_y, id_h) > 0$ / MDHGLM: $\sigma^2_{id_{y,m}}$ and $\sigma^2_{id_{h,m}}$ are large and $cov(id_{y,m}, id_{h,m}) > 0$ and all the other (co)variances = 0). Animals would hence choose an oikotype based on their genotypic particularities or on experience acquired before the use.

In a well-adapted populations, every phenotype should settle in its optimal habitat, the habitat that gives it the highest fitness possible. Such a situation represents a perfect matching habitat use (Edelaar *et al.* 2008) which may never be reached for different reasons. First, this is conceivable when *h* is stable over time (e.g., an individual settles in a habitat and stays there all its life), but may rarely be seen in more labile conditions, such as in a social habitat context. Second, organisms are made up of a large set of integrated traits experiencing

potential trade-offs with each other, and matching habitat use may be restricted if multiple ecologically relevant traits match with different oikotypic ranges. Moreover, the ability of an organism to detect habitat differences may be costly, and the multivariate nature of a habitat may force the individual to make compromises. Individuals may also not encounter the perfect habitat for their phenotype because it is unavailable or rare. Searching for the best habitat can be costly in time, energy, and increased predation risk, and given the uncertainty of finding the optimal habitat, individuals may rather choose to settle in a suboptimal one for their phenotypes (Davis & Stamps 2004). Finally, population density and intra- or interspecific competition may prevent an individual from perfectly matching the habitat with its phenotype. They may thus have to use other ways (i.e., plasticity or niche construction) of improving the fit between their habitat and their phenotypes.

With the second scenario (Figure 4b), individuals adjust their phenotypes as they change their oikotype for the habitat feature, or they move to a different oikotype as they change their phenotype for the trait, although they are still showing consistent differences in their phenotype and oikotype (MGLMM and MDHGLM, same as for Figure 4a but with $cov(e_y, e_h) \neq 0$). Here individuals are both more generalist ($\sigma^2_{e_h} > 0$) and more plastic in their trait ($\sigma^2_{e_y} > 0$) than in Figure 4a, while still showing strong segregation in both phenotype and oikotype.

In the third possible scenario (Figure 4c), individuals still differ consistently in their mean phenotype and oikotype but also show variance in plasticity and in the oikotypes they use (within-individual distribution of oikotypes). Plasticity decreases with the mean value of the phenotype and the oikotype. This scenario shows a population where individuals with different plasticity display different abilities for choosing a habitat. A possible trade-off

between plasticity and habitat use, forcing individuals to specialise in the use of one or the other option, may also explain this scenario. The evolution of adaptive phenotypic plasticity is possible through the evolution of individual abilities to detect cues in the environment that help them predict how to adjust their phenotype to improve their fitness given the environmental conditions. In scenario 4c, highly plastic individuals (Figure 4c) are not picky in the use of their habitat features (i.e., generalists), whereas highly picky individuals (top right), investing in the machinery necessary for picking the best oikotypes, can avoid being plastic (i.e., specialists). The trade-off between plasticity and habitat use may thus constrain an individual to be either a generalist or a specialist, depending on the conditions it encounters. This scenario could also reveal phenotype-dependent habitat use, potentially caused by intraspecific competition. For example, individuals with high phenotypic values (Figure 4c) can select the habitat with high oikotypic values (higher quality habitat) that matches their phenotype. They thus do not have to be plastic and can be specialists. In contrast, individuals with lower phenotypic values are constrained to use habitat with lower oikotypic values (lower quality habitat) and need to be more plastic to fit with the higher range of oikotypic values they experience. In the first case, we may expect identical fitness outcomes for the different options used here and a fitness ridge for the different phenotype and oikotype combinations, while in the second, we may see directional selection on both the trait and the habitat feature used.

The last scenario (Figure 4d) represents generalists, which can use both most of the full range of oikotypes and show most of the range of phenotypes available to the population. In this scenario, all the variance and covariance estimates are essentially zero, except for the within-individual variances and covariance. In this case, individuals may do equally well, but we can expect coevolution between the expressed phenotype for the labile trait and the chosen

oikotype for the labile habitat feature.

6. **Data requirements, feasibility of data collection and experiments**

In Figure 2, we outline the sample sizes and experimental design recommended to use the different modelling types. We discuss what types of data are appropriate and well suited to these analyses, focussing on analyses where individuals use different habitats. In theory, any trait-habitat covariation can be modelled. However, we recommend testing hypotheses grounded in biological theory. For example, animals with different body sizes and body conditions may not distribute randomly in the environment, which may affect resource availability. Physiological adaptations such as changes in colour occur in response to the environment and movement traits are commonly associated with habitat. Alongside these variables, any aspect of habitat can be modelled, be it abiotic, biotic or social, providing it can be measured alongside trait values.

Although a variety of data collection methods can be used, they may be more or less suitable for answering different questions. Experimentally manipulated systems can ensure large enough samples and balanced data. By blocking some causal pathways, they can let researchers infer causal mechanisms explaining the phenotype-oikotype correlation. Automated data collection, using equipment such as biologgers or recording systems, can collect relatively unbiased data in large volumes. These methods collect many repeated measures per individuals, which is ideal for the models we propose. Observational data can also be used, but the person's power required to collect these data may limit the sample sizes and repeats within individuals. Maximising the number of individuals and the number of repeats per individuals will generate the best data for these analyses. While collecting data

590 over long-time frames is ideal, we should restrict our interpretation of the results to the time
591 frame studied.
592
593 Consider that not many, if any, individuals may show the whole phenotypic variation of a trait
594 and may use the full range of habitat values of its population. A particularly pertinent
595 extension of our models would be the integration of habitat selection into the models of
596 habitat use. However, for simplification, we here assume that all individuals have access to
597 the same habitat. Modelling habitat availability relies on the ability to sample the available
598 habitats. While this can be done manually, satellite data perhaps offers the best opportunity to
599 sample unused areas. We hope that the framework and models presented in this paper inspire
600 others to build on our models to allow the availability of habitat or a possible range of trait
601 values to be included (see section 7 for discussion).
602
603 The models presented above, facilitate conceptualising the links between phenotypic
604 plasticity, habitat use, or niche construction that could occur within populations, and by
605 extension the eco-evolutionary reasons of the differences observed between populations. It is
606 important, however, to note that the modelling approaches we propose may exhibit limitations
607 in accurately partitioning variance components and disentangling causal mechanisms in
608 systems characterised by restricted dispersal capabilities—such as those with a high
609 proportion of philopatric individuals or inherently short dispersal distances. When coupled
610 with pronounced spatial heterogeneity, these conditions can generate substantial phenotype–
611 environment covariation, potentially confounding inference regarding the relative
612 contributions of phenotypic plasticity *versus* habitat use (see Gervais *et al.* 2022).
613
614 Also, there is no doubt that these models ideally require large data sets, with many repeated

615 measurements of phenotypic and oikotypic measures (e.g., more than 10 per individual) for a
616 significant number of individuals (e.g., at least 50). Figure 2 provides a helpful decision tree
617 to consider which model can be applied based on the data and the question and section 5
618 discusses which data may be suitable for these analyses. Certain fields have promising data to
619 answer these questions, and specifically biologging data sets could be appropriate for such
620 analyses (Kays *et al.* 2015).
621
622 When possible, combining these models and data with new experiments could provide a
623 strong approach to decipher the causes of the patterns of (co)variation between oikotypes and
624 phenotypes. For example, in Figure 4a, because individuals occupy a very limited oikotypic
625 range, it would likely be impossible to evaluate the level of plasticity of individuals. Running
626 a reciprocal transplant experiment would help assess the relative contribution of matching
627 habitat use and non-expressed phenotypic plasticity to the observed covariance between
628 phenotypes and oikotypes. The covariance between phenotypes and oikotypes observed after
629 moving individuals to a different oikotype can be attributed to phenotypic plasticity.
630 Alternatively, the covariance between phenotypes and oikotypes observed after allowing
631 individuals of known phenotypes to settle in the oikotype of their use can be attributed to
632 matching habitat use.
633
634 Finally, if individuals modify the oikotype they have been transplanted into (if possible), it
635 suggests niche construction. Phenotypic engineering experiments could also be fruitful to
636 understand the role of niche construction or habitat use (Camacho *et al.* 2020). If individuals
637 change their oikotype in response to a change in their phenotype, this suggests an important
638 role of habitat use or niche construction in driving the covariance between phenotypes and
639 oikotypes. However, if individuals do not change their oikotypes in response to a change in

their phenotype, this suggests that the covariance between phenotype an oikotype is not caused by matching habitat use or niche construction or that selection on habitat matching acts at a different time or life stage, prohibiting change. Similarly, oikotypic engineering experiments could bring important insights (i.e. Erixon, Krämer, Eccard, Gilmour & Dammhahn unpublished data). If after experimentally modifying local habitat conditions, individuals move to use a habitat with an oikotype similar to their original oikotype, this suggests that matching habitat use is prominent. If on the contrary, individuals change their phenotype while they do not change place, this indicates that they mostly rely on plasticity to match their phenotype with their oikotype.

7. Discussion

In this paper we present methods for modelling the covariation between an organism's traits and its habitat features: 1) phenotypic plasticity in response to change in the oikotype experienced, 2) use of specific oikotypic values matching with the phenotype, and 3) modification of habitat features to reach specific oikotypic values matching with the phenotype (niche construction). We show the complexity and richness of the information that these models provide. The modelling approaches we propose may be the first step to study the factors leading to the covariation and coevolution between phenotypic traits and their oikotypes. Moreover, combined with experiments they will allow us to study the different ways in which individuals deal with changing environments, will help us explain how and why these three processes can coexist within populations, and how their combination can favour the individual and genetic variation in many traits in wild populations subject to natural selection.

664 **7.1. Modelling oikotypes**

665 We propose a series of modelling techniques that can capture aspects of an individuals'
666 phenotype and oikotype. Multivariate mixed models (MGLMM) are the simplest model type,
667 owing to their ease of implementation in commonly used statistical packages. They allow us
668 to partition phenotypic and oikotypic variances into among and within-individual
669 components, and to assess their covariance to quantify whether the population globally
670 achieves phenotype-oikotype matching. These models have also been proposed by Munar-
671 Delgado *et al.* (2023) in a quantitative genetic framework. However, MGLMMs are limited in
672 three main ways. First, they cannot measure directly the phenotypic plasticity in response to
673 habitat; they can only estimate the covariation between phenotypes and oikotypes at the
674 among or within-individual level. Second, they cannot estimate among individual variation in
675 phenotype-oikotype covariance thus providing only a population level average estimate.
676 Third, within-individual (i.e. residual) covariance can reveal indiscriminately phenotypically
677 plastic changes due to oikotypic changes (either individuals move into a new habitat with a
678 different oikotypic value or modifies its local oikotype), phenotype-oikotype covariation due
679 to unmeasured external factors and covariation in measurement errors. Researchers should,
680 thus, make sure that combined measurement errors do not explain most of the (co)variance at
681 the residual level. These models do not provide an accurate measurement of the change in
682 phenotype in response to oikotype and do not estimate among-individual variation in it.
683 MGLMM can be fitted in R via multiple packages using either a frequentist (e.g. lme4, Bates
684 *et al.* 2015; ASReml, Gilmour *et al.* 1995) or Bayesian approach (e.g. brms, Bürkner 2017;
685 MCMCglmm Hadfield 2010; rjags, Plummer 2025).
686
687 Double-hierarchical models (DHGLM) are less frequent in ecology, and can be more
688 challenging to fit, but they extend the analyses that are possible with multivariate mixed

689 models to include individual level differences in variance components (Cain *et al.* 2023;
690 Jolles *et al.* 2019; O'Dea *et al.* 2022). This is an important improvement, as unmeasured
691 plasticity is captured in the variance components and thus parsed from the variance due to
692 measurement error. Accounting for individual differences in residual variance makes it
693 possible to infer plasticity at the individual level. Individuals that are more plastic would have
694 a larger within-individual variance in phenotype. This should be interpreted with caution,
695 though, as it can also capture maladaptive changes and associated mismatches (Martin *et al.*
696 2017). An increase in within-individual variance in oikotype would suggest that more plastic
697 individuals use or are exposed to a greater range of environments, and this can be used to
698 measure habitat specialisation. However, despite these modelling improvements, these models
699 are still unable to measure plasticity directly in response to the environment and do not
700 estimate among-individual variation in plasticity either. DHGLM can be fitted in R, for
701 example via ASReml (Gilmour *et al.* 1995), hglm (Ård *et al.* 2010) or using brms, stan and
702 JAGS.
703
704 Causal structure mixed models (CSMM) allow us to quantify phenotypic plasticity directly,
705 alongside changes in phenotype and oikotype, but are more complex to fit. This means we can
706 quantify individual differences in phenotype, oikotype, and the change in phenotype in
707 response to the habitat. However, it would be possible to fit models combining plasticity,
708 habitat use, and niche construction but would require much more complex data. CSMM
709 cannot be easily run in commonly used statistical packages but can be fitted in R with stan via
710 brms (Bürkner 2017) if the data of phenotype and oikotype are measured at the same time or
711 directly in stan if not.
712
713 **7.2. Breadth of questions**

Our models and results are of interest across a range of ecological and evolutionary questions, as the definition of habitat can be broad and cover a range of fields. DHGLMs and CSMM quantify individual level trait variances, which can be used to assess individual specialisation. The ability of DHGLMs (Westneat *et al.* 2015) and CSMM to quantify individual level differences is strong. It is widely accepted that a failure to model individual level effects can mask population-level patterns, but the models also allow the study of among- and within-individual differences to be extended to include phenotype-oikotype interactions. As habitat influences resource acquisition and risk avoidance, it is linked to life-history trade-offs and so may be a crucial part of the pace-of-life syndrome (Hamalainen *et al.* 2021; Montiglio *et al.* 2018; Polverino *et al.* 2018) suggesting habitat use should be integrated into this framework (Smallegange & Guenther 2025)**.**

Modelling the observed variation in nature can help design experiments to test predictions and the mechanisms behind the variation we see. While not the focus of this paper, niche construction can also be assessed using these models. Measurements of among-individual variation in niche construction can be estimated even without fine-scale temporal data, and individual differences in niche construction can be modelled if sufficient data is available. Niche construction would be detected as low variation in oikotype, and if the phenotype correlates with the propensity to adjust habitat or habitat itself, there should be a covariation between the phenotype and the oikotype.

The approach presented here is, of course, not limited to one trait and one oikotype and can be extended to multiple oikotypes related to one trait, multiple traits related to one oikotype and even multiple traits related to multiple oikotypes (Martin 2025). It can also examine the importance of variation in oikotype and phenotype over different life stages, testing whether

739 the optimal strategy for individuals changes over time (Takola & Schielzeth 2022). One
740 important way this could be used is to estimate natural selection for the trait and the oikotype.
741 Such objectives would require estimating the covariance between fitness and phenotype and
742 oikotype at the among-individual level. This can be done in multiple ways depending on the
743 structure of the data. One way to estimate natural selection, potentially the one with the most
744 power, would be to extend the causal structure approach by including a third model fitting
745 fitness as a function of the oikotype and/or the phenotype. Alternative approaches include
746 fitting fitness as a third trait in a multivariate approach and deriving a selection gradient from
747 the (co)variance matrix at the among-individual level (e.g. Dingemanse *et al.* 2021; Videlier
748 *et al.* 2020) or extracting the BLUPs for the phenotype and the oikotype and including
749 estimates of individual reproductive performance (carrying forward the uncertainty; see
750 Hadfield *et al*. (2010)), or alternatively to use an error-in-variables model (Dingemanse *et al.*
751 2021). If matching habitat use occurs, a correlation between phenotype and oikotype would
752 result in higher fitness for all individuals (i.e. correlational selection). If some individuals are
753 forced into habitats, for example through competition, the covariation between oikotype and
754 phenotype would range from low to high fitness across phenotypic-oikotype combinations.
755 Capturing habitat variation is often tricky in the wild, as we have incomplete knowledge of
756 which habitat variables individuals respond to, and so our measure of oikotype may not be
757 representative of the key habitat selection decisions. First, while modelling multiple habitats
758 seems optimal, the added complexity and computer processing required to fit such models
759 might not be feasible. Second, the current modelling techniques do not allow us to account for
760 habitat availability. Resource selection functions (RSFs) estimate the strength of habitat
761 selection given the available habitat (Lele *et al.* 2013). While they do not estimate used
762 habitat, and hence oikotype, they are able to estimate the strength of individual preference
763 (Muff *et al.* 2020) and account for habitat rarity (Fokkema *et al.* 2021). Future iterations of

764 these models should attempt to incorporate RSFs.

765

766 **7.3 Extension to incorporate habitat availability and selection**

767 The focus of this framework is to quantify the portion of the population habitat range (or
768 environmental variation) expressed by individuals. We assume that all individuals can access
769 all habitats. Note that ecological processes such as competition may exclude them from some,
770 but this would explain the phenotypic-oikotypic correlation in the same way as matching
771 habitat use. What is crucial to understand is the mean and variance in the oikotype and hence
772 used habitat in relation to individual phenotypes. Just as there may be unmeasured potential
773 phenotypes, there may be unmeasured oikotypes not quantified using this method, but the
774 focus is on the phenotype-oikotype covariation in the population, what it tells us about the
775 eco-evolutionary processes that lead to non-random distribution of individuals in the
776 environment and the consequences of this (co)variation for the population. The availability of
777 habitats is an important, but distinctly different question. While not necessary to incorporate
778 into the framework we propose, as we start to think about the drivers of oikotypic variation,
779 the available habitat becomes a potentially important factor (Fokkema *et al.* 2021).

780

781 To explore possible oikotypes, studies need to sample from a pool of feasible, unused
782 oikotypes. Using logistic regression or generalised linear models, habitat selection analyses
783 compare the oikotypes of an individual against a range of accessible locations and habitats.
784 These estimate the preferred oikotype of an individual, given what is available. They have
785 been widely used and recent studies have included individual variation into these models by
786 fitting random slopes to allow individuals to differ in the direction and strength of habitat
787 selection (Muff *et al.* 2020). The covariation between phenotypes and oikotypes does not tell
788 us about individual choice, and habitat selection models can quantify preference. Combining

789 these models could help tease apart whether individuals express their ideal oikotype. Habitat
790 selection models can also use individual level estimates of the available habitat to estimate the
791 potential oikotype of an individual (Lele *et al.* 2013). In a changing environment these models
792 may add important information when predicting adaptation to change.
793
794 There are some straightforward workarounds to incorporate habitat selection such as
795 including the average or the range of habitats available at the population and individual levels
796 as fixed effects in causal structure models suggested above. This could be estimated from a
797 spatial grid, as in habitat selection models, or as the population or individual average and
798 range of oikotype observed. This would offer a simplified habitat availability estimate and
799 could be included in subsequent models to assess the deviation from the preferred habitat
800 versus oikotype. A further extension would be to include resource-selection (RSF) or step-
801 selection (SSF) functions considering individual heterogeneity in the causal structure model.
802 This can be done in a few different ways depending on the data and the exact question of
803 interest. For example, one can add a SSF (or RSF) model as a third model in the CS model
804 allowing to estimate individual deviation between the predicted preferred habitat (estimated
805 from the RSF/SSF) and the realised habitat used estimated from the oikotype model.
806
807 However, while accounting for habitat availability can be important, RSF and SSF still rely
808 on assumptions about what habitat is available at the individual level. Phenotype-oikotype
809 correlations may constrain an individual's access to certain habitats. For example, very large
810 individuals may not be able to feed in very shallow waters and therefore the habitat available,
811 and the strength of habitat selection, may be overestimated. Researchers must think carefully
812 about what habitat is available to an individual and how this may be affected by phenotype-
813 oikotype correlations. One extension of the model if including RSF/SSF with the framework

814 is that it is feasible to include the phenotype in the habitat selection model, thus estimating
815 how the phenotype impacts the habitat preference, and how the habitat used impact the
816 phenotype. Moreover, an exciting extension to the framework is the importance of habitat
817 availability on phenotype-oikotype covariation. Do individuals show more variable oikotypes
818 when their preferred habitat is rare? Is phenotypic plasticity less common if there is enough
819 preferred habitat close by? Is it available habitat that drives the fitness landscape around
820 oikotype-phenotype interactions? In a changing environment these questions become more
821 pertinent, and we encourage other researchers to explore how to incorporate these ideas into
822 models.
823

824 **8. Concluding remarks**

825 While the data required for the models we describe may be challenging to obtain,
826 understanding the key parameters and the processes they highlight is crucial, even when
827 studying phenotypic plasticity and habitat use independently. Simulations may offer the most
828 effective next step toward understanding the relative importance of phenotypic plasticity and
829 habitat use in different environments, as widespread changes to habitats affect not only the
830 physical environment but also the social environment. Changes in population size and the
831 frequency of individual strategies can alter the adaptive benefits of currently observed
832 patterns; thus, modelling these individual strategies is essential for predicting their persistence
833 over time. As environmental change significantly impacts habitat availability, understanding
834 the interplay between phenotypic plasticity and habitat use is key to predicting the potential
835 for future adaptation.
836

837 **9. References**

838 Akcali, C.K. & Porter, C.K. (2017). Comment on Van Belleghem et al. 2016: Habitat choice
839 mechanisms in speciation and other forms of diversification. *Evolution*, 71, 2754–2761.

Araya-Ajoy, Y.G. & Dingemanse, N.J. (2017). Repeatability, heritability, and age-dependence of seasonal plasticity in aggressiveness in a wild passerine bird. *Journal of Animal Ecology*, 86, 227–238.

Ård, L., Shen, X. & Alam, M. (2010). hglm: A Package for Fitting Hierarchical Generalized Linear Models. *The R Journal*, 2, 20–28.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.

Block, W.M. & Brennan, L.A. (1993). The Habitat Concept in Ornithology. *Current Ornithology*, 35–91.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., *et al.* (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161, 1–28.

Brommer, J.E., Merila, J., Sheldon, B.C. & Gustafsson, L. (2005). Natural selection and genetic variation for reproductive reaction norms in a wild bird population. *Evolution*, 59, 1362–1371.

Bürkner, P.-C. (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, 80, 1–28.

Cain, S., Solomon, T., Leshem, Y., Toledo, S., Arnon, E., Roulin, A., *et al.* (2023). Movement predictability of individual barn owls facilitates estimation of home range size and survival. *Movement Ecology*, 11, 10.

Camacho, C., Sanabria-Fernández, A., Baños-Villalba, A. & Edelaar, P. (2020). Experimental evidence that matching habitat choice drives local adaptation in a wild population. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20200721.

Cleasby, I.R., Nakagawa, S. & Schielzeth, H. (2015). Quantifying the predictability of behaviour: statistical approaches for the study of between-individual variation in the within-individual variance. *Methods in Ecology and Evolution*, 6, 27–37.

Davis, J.H. (1960). Proposals Concerning the Concept of Habitat and A Classification of Types. *Ecology*, 41, 537–541.

Davis, J.M. & Stamps, J.A. (2004). The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution*, 19, 411–416.

Dawkins, R. (1982). *The Extended Phenotype: The Long Reach Of The Gene*. Oxford University Press, Oxford.

De Jong, G. (2005). Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytologist*, 166, 101–118.

DeWitt, T.J. (1998). Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *Journal of Evolutionary Biology*, 11, 465–480.

DeWitt, T.J., Sih, A. & Wilson, D.S. (1998). Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution*, 13, 77–81.

879 Dingemanse, N.J., Araya-Ajoy, Y.G. & Westneat, D.F. (2021). Most published selection
880 gradients are underestimated: Why this is and how to fix it. *Evolution*, 75, 806–818.

881 Dingemanse, N.J. & Réale, D. (2022). Evolutionary Behavioural Ecology Perspectives on
882 Personality in Non-Human Animals. *The Routledge International Handbook of Comparative*
883 *Psychology*, 289–301.

884 Edelaar, P. & Bolnick, D.I. (2019). Appreciating the Multiple Processes Increasing Individual
885 or Population Fitness. *Trends in Ecology & Evolution*, 34, 435–446.

886 Edelaar, P., Jovani, R. & Gomez-Mestre, I. (2017). Should I Change or Should I Go?
887 Phenotypic Plasticity and Matching Habitat Choice in the Adaptation to Environmental
888 Heterogeneity. *The American Naturalist*, 190, 506–520.

889 Edelaar, P., Siepielski, A.M. & Clobert, J. (2008). Matching habitat choice causes directed
890 gene flow: a neglected dimension in evolution and ecology. *Evolution*, 62, 2462–2472.

891 European Environment Agency. (2019). *EUNIS - European Nature Information System.*
892 Available at: https://eunis.eea.europa.eu/. Last accessed 2 May 2025.

893 Falconer, D.S. & Mackay, T.F.C. (1996). *Introduction to Quantitative Genetics*. Longman,
894 New York.

895 Fokkema, R.W., Korsten, P., Schmoll, T. & Wilson, A.J. (2021). Social competition as a
896 driver of phenotype–environment correlations: implications for ecology and evolution.
897 *Biological Reviews of the Cambridge Philosophical Society*, 96, 2561–2572.

898 Geremia, C., Merkle, J.A., Eacker, D.R., Wallen, R.L., White, P.J., Hebblewhite, M., *et al.*
899 (2019). Migrating bison engineer the green wave. *Proceedings of the National Academy of*
900 *Sciences*, 116, 25707–25713.

901 Gervais, L., Morellet, N., David, I., Hewison, M., Réale, D., Goulard, M., *et al.* (2022).
902 Quantifying heritability and estimating evolutionary potential in the wild when individuals
903 that share genes also share environments. *Journal of Animal Ecology*, 91, 1239–1250.

904 Gianola, D. & Sorensen, D. (2004). Quantitative Genetic Models for Describing Simultaneous
905 and Recursive Relationships Between Phenotypes. *Genetics*, 167, 1407–1424.

906 Gilmour, A.R., Thompson, R. & Cullis, B.R. (1995). Average Information REML: An
907 Efficient Algorithm for Variance Parameter Estimation in Linear Mixed Models. *Biometrics*,
908 51, 1440–1450.

909 Hadfield, J.D. (2010). MCMC methods for multi-response generalized linear mixed models:
910 the MCMCglmm R package. *Journal of Statistical Software*, 33, 1–22.

911 Hadfield, J.D., Wilson, A.J., Garant, D., Sheldon, B.C., Kruuk, L.E.B. & Shaw, A.E. and
912 E.R.G. (2010). The Misuse of BLUP in Ecology and Evolution. *The American Naturalist*,
913 175, 116–125.

914 Hall, L. S., Krausman, P. R., & Morrison, M. L. (1997). The habitat concept and a plea for
915 standard terminology. *Wildlife Society Bulletin*, 25(1), 173–182.

916 Hamalainen, A.M., Guenther, A., Patrick, S.C. & Schuett, W. (2021). Environmental effects
917 on the covariation among pace-of-life traits. *Ethology*, 127, 32–44.

Hamilton, I.M. (2017). Habitat Selection. In: *Reference Module in Life Sciences*. Elsevier.

Holtmann, B., Lagisz, M. & Nakagawa, S. (2017). Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: a meta-analysis. *Functional Ecology*, 31, 685–696.

IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES secretariat, Bonn, Germany.

Jablonszky, M. & Garamszegi, L.Z. (2024). The effect of repeated measurements and within-individual variance on the estimation of heritability: a simulation study. *Behavioral Ecology and Sociobiology*, 78, 18.

Jacob, S., Bestion, E., Legrand, D., Clobert, J. & Cote, J. (2015). Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. *Evolutionary Ecology*, 29, 851–871.

Jaenike, J. & Holt, R.D. (1991). Genetic Variation for Habitat Preference: Evidence and Explanations. *The American Naturalist*, 137, S67–S90.

Johnson, M.D. (2007). Measuring Habitat Quality: A Review. *The Condor*, 109, 489–504.

Jolles, J.W., Briggs, H.D., Araya-Ajoy, Y.G. & Boogert, N.J. (2019). Personality, plasticity and predictability in sticklebacks: bold fish are less plastic and more predictable than shy fish. *Animal Behaviour*, 154, 193–202.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348.

Laland, K.N., Uller, T., Feldman, M.W., Sterelny, K., Müller, G.B., Moczek, A., *et al.* (2015). The extended evolutionary synthesis: its structure, assumptions and predictions. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151019.

Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, 22, 1435–1446.

Lee, Y. & Nelder, J.A. (2006). Double hierarchical generalized linear models (with discussion). *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 55, 139–185.

Lele, S.R., Merrill, E.H., Keim, J. & Boyce, M.S. (2013). Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology*, 82, 1183–1191.

Lewontin, R.C. (1983). The Organism as the Subject and Object of Evolution. *Scientia*, 118, 63–82.

Lowe, W.H. & Addis, B.R. (2019). Matching habitat choice and plasticity contribute to phenotype–environment covariation in a stream salamander. *Ecology*, 100.

Lynch, C.B. (1980). Response to divergent selection for nesting behavior in Mus musculus. *Genetics*, 96, 757–765.

Martin, J.G.A., Pirotta, E., Petelle, M.B. & Blumstein, D.T. (2017). Genetic basis of between-individual and within-individual variance of docility. *Journal of Evolutionary Biology*, 30, 796–805.

Martin, J.S. (2025). Covariance reaction norms: A flexible method for estimating complex environmental effects on trait (co)variances. *Methods in Ecology and Evolution*, 16, 2098–2117.

Matthiopoulos, J., Fieberg, J.R. & Aarts, G. (2023). Species-Habitat Associations: Spatial data, predictive models, and ecological insights, 2nd Edition.

Mayor, S., Schneider, D., Schaefer, J. & Mahoney, S. (2009). Habitat Selection at Multiple Scales. *Ecoscience*, 16, 238–247.

McComb, B.C. (2007). *Wildlife Habitat Management*. CRC Press, Boca Raton.

Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., *et al.* (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160456.

Montgomery, R.A. & Roloff, G.J. (2013). Habitat Selection. *Encyclopedia of Biodiversity*, 59–69.

Montiglio, P.-O., Dammhahn, M., Dubuc Messier, G. & Réale, D. (2018). The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology*, 72.

Muff, S., Signer, J. & Fieberg, J. (2020). Accounting for individual-specific variation in habitat-selection studies: Efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, 89, 80–92.

Munar-Delgado, G., Araya-Ajoy, Y.G. & Edelaar, P. (2023). Estimation of additive genetic variance when there are gene–environment correlations: Pitfalls, solutions and unexplored questions. *Methods in Ecology and Evolution*, 14, 1245–1258.

Munar-Delgado, G., Pulido, F. & Edelaar, P. (2024). Performance-based habitat choice can drive rapid adaptive divergence and reproductive isolation. *Current Biology*, 34, 5564-5569.e4.

Nicolaus, M. & Edelaar, P. (2018). Comparing the consequences of natural selection, adaptive phenotypic plasticity, and matching habitat choice for phenotype–environment matching, population genetic structure, and reproductive isolation in meta-populations. *Ecology and Evolution*, 8, 3815–3827.

Northrup, J.M., Vander Wal, E., Bonar, M., Fieberg, J., Laforge, M.P., Leclerc, M., *et al.* (2022). Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. *Ecological Applications*, 32, e02470.

O'Dea, R.E., Noble, D.W.A. & Nakagawa, S. (2022). Unifying individual differences in personality, predictability and plasticity: A practical guide. *Methods in Ecology and Evolution*, 13, 278–293.

Pfennig, D.W. (2021). *Phenotypic Plasticity & Evolution*. CRC Press, Boca Raton.

995 Plummer, M. (2025). rjags: Bayesian Graphical Models using MCMC. R package version 4-
996 17.

997 Polverino, G., Santostefano, F., Díaz-Gil, C. & Mehner, T. (2018). Ecological conditions
998 drive pace-of-life syndromes by shaping relationships between life history, physiology and
999 behaviour in two populations of Eastern mosquitofish. *Scientific Reports*, 8, 14673–14673.

1000 Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007). Integrating
1001 animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318.

1002 Rosenzweig, M.L. (1991). Habitat Selection and Population Interactions: The Search for
1003 Mechanism. *The American Naturalist*, 137, S5–S28.

1004 Saltz, J.B. & Nuzhdin, S.V. (2014). Genetic variation in niche construction: implications for
1005 development and evolutionary genetics. *Trends in Ecology & Evolution*, 29, 8–14.

1006 Scheiner, S.M. (2016). Habitat Choice and Temporal Variation Alter the Balance between
1007 Adaptation by Genetic Differentiation, a Jack-of-All-Trades Strategy, and Phenotypic
1008 Plasticity. *The American Naturalist*, 187, 633–646.

1009 Shoji, A., Owen, E., Bolton, M., Dean, B., Kirk, H., Fayet, A., *et al.* (2014). Flexible foraging
1010 strategies in a diving seabird with high flight cost. *Marine Biology*, 161, 2121–2129.

1011 Smallegange, I.M. & Guenther, A. (2025). A development-centric perspective on pace-of-life
1012 syndromes. *Evolution Letters*, 9, 172–183.

1013 Stamps, J.A. & Davis, J.M. (2006). Adaptive effects of natal experience on habitat selection
1014 by dispersers. *Animal Behaviour*, 72, 1279–1289.

1015 Takola, E. & Schielzeth, H. (2022). Hutchinson's ecological niche for individuals. *Biological*
1016 *Philosophy*, 37, 25.

1017 Trappes, R., Nematipour, B., Kaiser, M.I., Krohs, U., van Benthem, K.J., Ernst, U.R., *et al.*
1018 (2022). How Individualized Niches Arise: Defining Mechanisms of Niche Construction,
1019 Niche Choice, and Niche Conformance. *Bioscience*, 72, 538–548.

1020 Turko, A.J. & Rossi, G.S. (2022). Habitat choice promotes and constrains phenotypic
1021 plasticity. *Biology Letters*, 18, 20210468.

1022 Varona, L. & González-Recio, O. (2023). *Invited review:* Recursive models in animal
1023 breeding: Interpretation, limitations, and extensions. *Journal of Dairy Science*, 106, 2198–
1024 2212.

1025 Videlier, M., Careau, V., Wilson, A.J. & Rundle, H.D. (2020). Quantifying selection on
1026 standard metabolic rate and body mass in Drosophila melanogaster. *Evolution*, 75, 130–140.

1027 Warwick-Evans, V., Atkinson, P.W., Arnould, J.P.Y., Gauvain, R., Soanes, L., Robinson,
1028 L.A., *et al.* (2016). Changes in behaviour drive inter-annual variability in the at-sea
1029 distribution of northern gannets. *Marine Biology*, 163, 156.

1030 Webber, Q.M.R., Albery, G.F., Farine, D.R., Pinter-Wollman, N., Sharma, N., Spiegel, O., *et*
1031 *al.* (2023). Behavioural ecology at the spatial–social interface. *Biological Reviews*, 98, 868–
1032 886.

1033 Wecker, S.C. (1964). Habitat Selection. *Scientific American*, 211, 109–116.

1034 Westneat, D.F., Wright, J. & Dingemanse, N.J. (2015). The biology hidden inside residual
1035 within-individual phenotypic variation. *Biological Reviews*, 90, 729–743.

1036 Whittaker, R.H., Levin, S.A. & Root, R.B. (1973). Niche, Habitat, and Ecotope. *The*
1037 *American Naturalist*, 107, 321–338.

1038 Table 1: Estimates from a causal structure DHGLM of Selkie aggressiveness (*i.e.* the focal

1039 phenotypic trait) and water temperature (*i.e.* the focal oikotype trait).

Parameter	Parameter	Median	HPDI (95%)	Interpretation
	Aggressiveness			
β_{y0}	Mean part: Intercept	-0.022	-0.23/0.187	Average mean aggressiveness
β_h	**Mean part: Temperature**	**0.870**	**0.722/1.027**	**Increased aggressiveness in warmer water**
$\beta_X X_{ij}$	**Mean part: Sex**	**0.389**	**0.06/0.708**	**Females more aggressive**
γ_{y0}	Sigma part: Intercept	-0.006	-0.192/0.171	Average variance in aggressiveness
$\gamma_X X_{ij}$	**Sigma part: Sex**	**0.367**	**0.106/0.62**	**Females more variable in aggressiveness**
	Temperature			
β_{h0}	Mean part: Intercept	0.075	-0.094/0.23	Average mean water temperature used
γ_{h0}	Sigma part Intercept	-0.010	-0.074/0.065	Average variance in water temperature used
	Variance components			
α_{y,m_i}	**Var(Aggressiveness mean)**	**0.207**	**0.1/0.379**	**Individual differences in mean aggressiveness**
α_{y,p_i}	**Var(Aggressiveness slope Temperature)**	**0.095**	**0.025/0.195**	**Individual differences in plasticity**
α_{y,v_i}	**Var(Aggressiveness dispersion)**	**0.209**	**0.115/0.336**	**Individual differences in variance in aggressiveness**
α_{y,v_i}	**Var(Temperature mean)**	**0.220**	**0.116/0.363**	**Individual differences in mean water temperature**
α_{h,v_i}	Var(Temperature dispersion)	0.003	0/0.019	No individual differences in variance in water temperature
	cor(Aggressiveness mean, Aggressiveness slope Temperature)	**0.667**	**0.274/0.943**	**More aggressive selkies were more plastic**
	cor(Aggressiveness mean, Temperature mean)	**0.693**	**0.375/0.954**	**More aggressive selkies were found in warmer waters**
	cor(Aggressiveness slope Temperature, Temperature mean)	**0.473**	**0.046/0.827**	**More plastic selkies were found in warmer waters**
	cor(Aggressiveness mean, Aggressiveness dispersion)	**-0.512**	**-0.803/-0.103**	**More aggressive selkies were less variable**
	cor(Aggressiveness slope Temperature, Aggressiveness dispersion)	-0.283	-0.708/0.163	No relationship between plasticity and variance in aggressiveness
	cor(Aggressiveness dispersion, Temperature mean)	**-0.618**	**-0.855/-0.318**	**Selkies with more variable aggressiveness were found in cooler waters**
	cor(Aggressiveness dispersion, Temperature dispersion)	-0.300	-0.865/0.49	No relationship between variance in aggressiveness and variance in water temperature

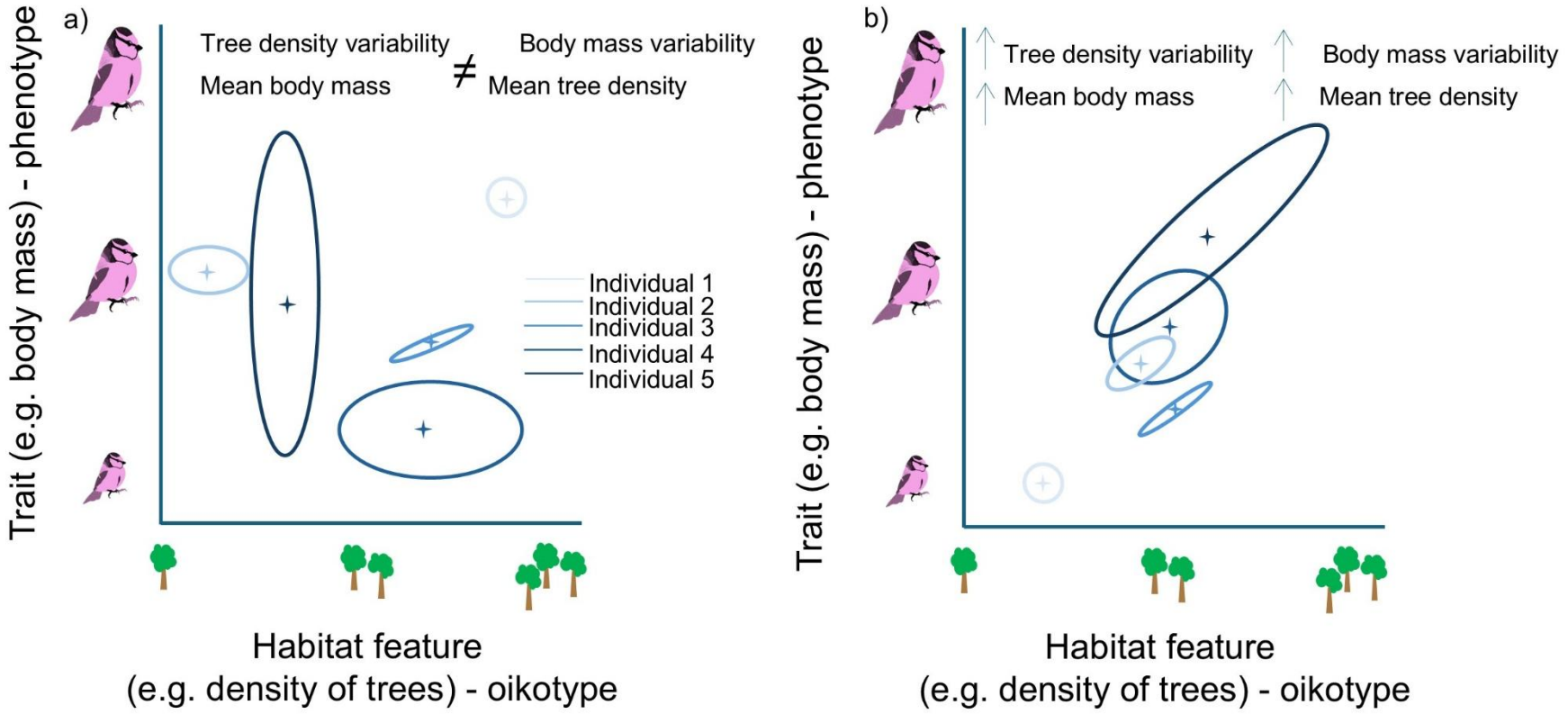
Parameter	Parameter	Median	HPDI (95%)	Interpretation
	cor(Aggressiveness mean, Temperature dispersion)	0.200	-0.511/0.892	No relationship between mean aggressiveness and variance in water temperature
	cor(Aggressiveness slope Temperature, Temperature dispersion)	0.057	-0.688/0.752	No relationship between plasticity and variance in water temperature
	cor(Temperature mean, Temperature dispersion)	0.224	-0.499/0.828	No relationship between mean and variance in water temperature

Notes: Mean and dispersion refer to the mean and dispersion parts of the DHGLM for both traits. Fixed effects and correlations for which the HPDI did not overlap zero are in bold. Variance parameters with a lower HPDI above 0.01 are also bolded. Models were fitted on 500 observations from 50 selkies with 10 measurements each. Parameters estimating the effect on aggressiveness are shown in blue; those estimating effects on temperature are in pink and those looking at the effects on both in green.

Text box 1: The "oikotype"

In this paper we propose a new term for habitat as an extended phenotype: the "oikotype". We define this as a measure of a feature of the habitat used by an individual. An oikotype can be considered as analogous to a phenotype, but for a habitat trait, rather than a trait within an organism's body. Some readers may wonder why we have created a neologism when we could have used phenotype, extended phenotype, or niche. There are several reasons why it is important. First, people will always distinguish between traits measured in an organism and the habitat features used by that organism. It is therefore more convenient to use the term "oikotype" than "phenotype for a habitat feature". Second, the concept of the oikotype is broader than Dawkins (1982) extended phenotype, as it makes no assumptions about the processes (e.g. use or construction) that lead to the phenotype- or genotype-oikotype correlation, about the adaptive function of these processes, or about the subjective classification of habitat value (e.g. quality). Researchers should bear in mind that phenotype-oikotype correlations could result from matching habitat use, or simply from processes such a

competitive exclusion, where based on their phenotype some individuals chose specific oikotypes preventing other individuals to use these oikotypes. Third, the oikotype concept avoids the anthropocentric bias inherent in the concept of habitat (e.g. what we categorise as two “habitats” may be perceived as one by animals). Finally, distinguishing the oikotype from the phenotype will help researchers to conceptualise questions concerning the non-random distribution of organisms in a heterogeneous environment. It is also important to recognise that organisms, and the habitat they use, are both multidimensional. Just as an individual can have multiple traits, a habitat that an individual chooses or uses can also have multiple features. Logistical and analytical limitations restrict the number of traits or habitat features that researchers can include in their study. However, we should always bear in mind that, just as one phenotypic measure of a trait does not define an organism, one oikotypic measure of a habitat feature does not define its niche.

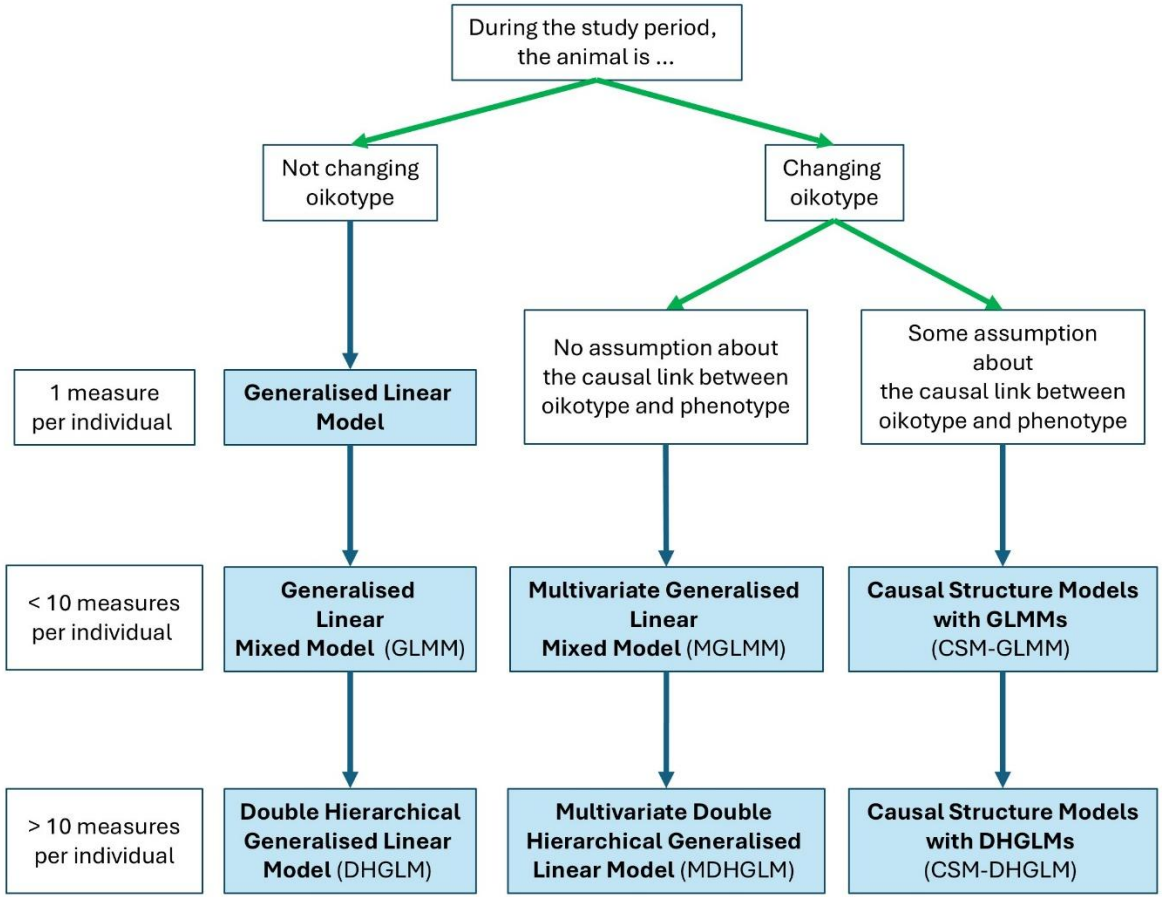


1075

1076 Figure 1. Schematic representation of the (co)variance between a trait and a habitat feature for individuals in a wild population. Here we consider

1077 a labile trait of an organism (body mass in pink birds, y-axis) and a labile feature of its habitat (density of trees, x-axis). The trait shows a

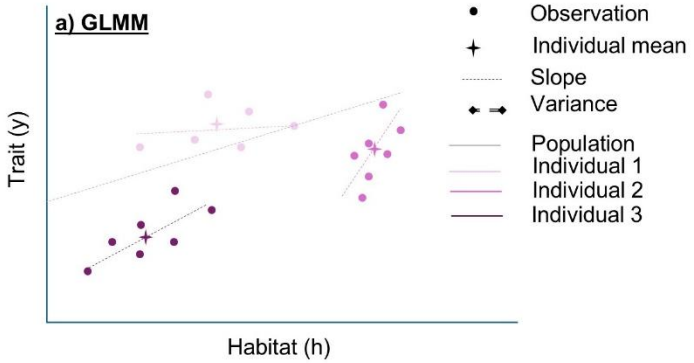
phenotypic variance (variance of the distribution of all the measures of the trait in the population- i.e. variance in the y axis). The habitat feature shows an oikotypic variance (variance of the distribution of all the measures of the habitat feature in the population - i.e. variance in the x axis). Each ellipse represents the (co)variation space of an individual repeatedly measured for its body mass, and the density of trees of the microhabitat it uses. The diamond at the centre of the ellipse is the estimated mean phenotype and oikotype for each individual. In this fictitious example, individuals do not express the whole oikotypic and phenotypic variation of their population. The width of the ellipse tells us how variable the individual is in the two dimensions. a) While specialists and generalist still exist in the population, there is no covariation between how variable birds are in the body mass and tree density and the degree of generalism does not predict body mass or habitat use. b) Individuals differ in their means and variance in body mass and tree density. Birds that vary in body mass also showing high variability in tree density and birds which are variable have lower mean body mass and use less dense habitat. The blue colours represent five different individuals. Bird drawing adapted from © 2025 Hélène Dion-Phénix.



1088

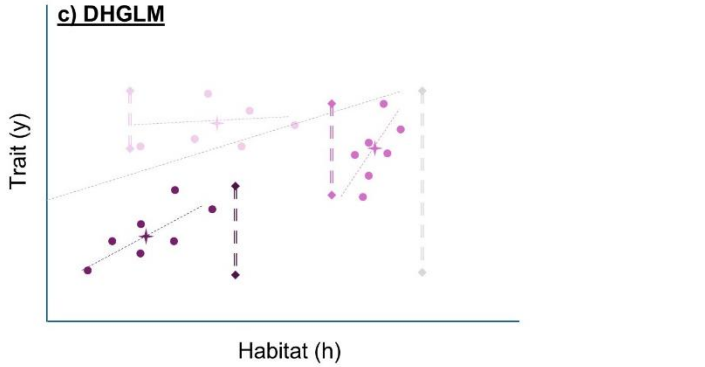
1089 Figure 2. Decision tree for studies that analyse the link between phenotype and oikotype, based on the data available and the

1090 hypotheses. Estimates of sample size come from simulation studies.



$$\boldsymbol{Eq.\,9}\text{: } y_{ij} = \sum_k \beta_k X_{k_{ij}} + (\beta_h + \alpha_{y,p_i}) h_{ij} + \alpha_{y,m_i} + e_{y_{ij}}$$

Population intercept and slope | Individual random slope | Individual random intercept

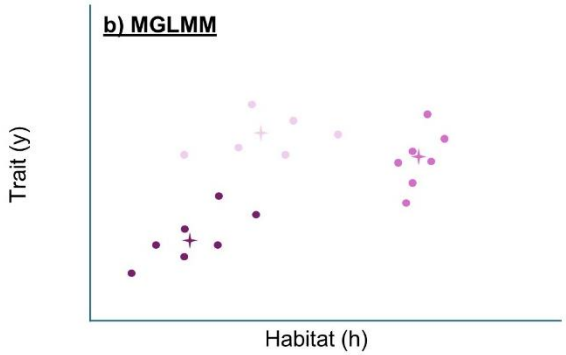


$$\boldsymbol{Eq.\,7a}\text{: } y_{ij} = \sum_k \beta_k X_{k_{ij}} + (\beta_h + \alpha_{y,p_i}) h_{ij} + \alpha_{y,m_i} + e_{y_{ij}} \text{ and}$$

Population intercept and slope | Individual random slope | Individual random intercept

$$ln(\sigma_{e_{y_{ij}}}) = \sum_l \gamma_l X_{l_{ij}} + \alpha_{y,v_i}$$

Population variance | Individual variance

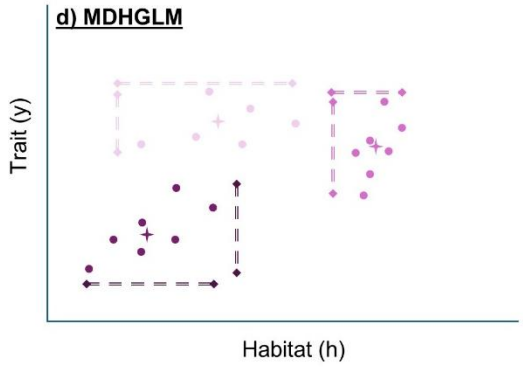


$$\boldsymbol{Eq.\,1a}\text{: } y_{ij} = \sum_k \beta_k X_{k_{ij}} + \alpha_{y,m_i} + e_{y_{ij}}$$

Population intercept | Individual random intercept

$$\boldsymbol{Eq.\,1b}\text{: } h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h,m_i} + e_{h_{ij}}$$

Population intercept | Individual random intercept



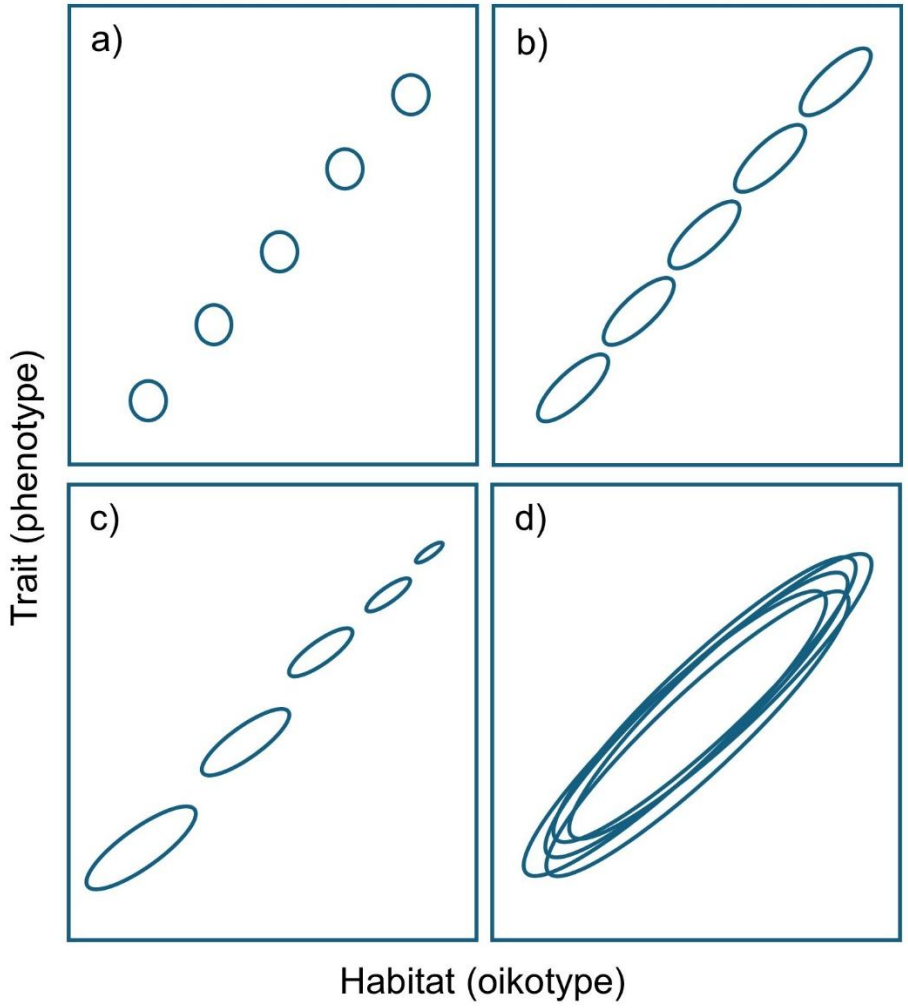
$$\boldsymbol{Eq.\,4a}\text{: } y_{ij} = \sum_k \beta_k X_{k_{ij}} + \alpha_{y,m_i} + e_{y_{ij}} \quad \text{and } ln(\sigma_{e_{y_{ij}}}) = \sum_l \gamma_l X_{l_{ij}} + \alpha_{y,v_i}$$

$$\boldsymbol{Eq.\,4b}\text{: } h_{ij} = \sum_n \beta_n X_{n_{ij}} + \alpha_{h,m_i} + e_{h_{ij}} \quad \text{and } ln(\sigma_{e_{y_{ij}}}) = \sum_o \gamma_o X_{o_{ij}} + \alpha_{h,v_i}$$

Population intercept | Individual random intercept | Population variance | Individual variance

1091

Figure 3. Schematic diagram illustrating the main parameters in each model type. For simplicity the covariance among traits are not displayed. a) A GLMM with the trait (y)- the phenotype fitted against a fixed effect of habitat (h). The model fits a random intercept and random slope. Habitat is not considered as a trait, but as an explanatory variable. This is a classic phenotypic plasticity model. Eq. 9 is not shown in the main paper but is presented here to demonstrate how our models build on this. Habitat is often mean centred in these models. b) A MGLMM where the trait (phenotype) and the habitat (oikotype) are modelled as response variables. Here the model estimates a mean for each individual in both the trait and the habitat. c) A DHGLM, building on a traditional GLMM (a), estimating the variance in the trait. This model includes random intercepts and slopes and estimates an individual parameter for the mean and variance. Habitat remains as an explanatory variable and the individual variance parameter is the residual variance after fitting random slopes – i.e. the variance after controlling for the effect of habitat. d) A MDHGLM fitting a multivariate model where the trait and the habitat are modelled as response variables. The model estimates a mean for the trait and habitat for each individual (as in b). This model estimates additional parameters for the variance for individuals in both the trait and the habitat. A CS-DHGLM which essentially combines a DHGLM (c) and a MDHGLM (d). The equations are Eq. 7a and Eq. 4b. It allows the estimation of individual random slopes in response to the habitat (phenotypic plasticity) and to estimate the individual mean and variance in both the trait and habitat. All equations are numbered as in the text. Full details of these equations can be found in the text. All models also estimate covariance parameters which estimate how these variables are associated with one another. Full covariance matrices can be seen in Figure 4.



(co)variance matrices

	Among-individual	Within-individual
	$\begin{bmatrix} \sigma^2_{id_{ym}} & \cdot & \cdot & \cdot \\ cov & \sigma^2_{id_{yv}} & \cdot & \cdot \\ cov & cov & \sigma^2_{id_{hm}} & \cdot \\ cov & cov & cov & \sigma^2_{id_{hv}} \end{bmatrix}$	$\begin{bmatrix} \sigma^2_{e_y} & \cdot \\ cov & \sigma^2_{e_h} \end{bmatrix}$
A'	$\begin{bmatrix} \gg 0 & \cdot & \cdot & \cdot \\ 0 & 0 & \cdot & \cdot \\ > 0 & 0 & \gg 0 & \cdot \\ 0 & 0 & 0 & 0 \end{bmatrix}$	$\begin{bmatrix} > 0 & \cdot \\ 0 & > 0 \end{bmatrix}$
B'	$\begin{bmatrix} \gg 0 & \cdot & \cdot & \cdot \\ 0 & 0 & \cdot & \cdot \\ > 0 & 0 & \gg 0 & \cdot \\ 0 & 0 & 0 & 0 \end{bmatrix}$	$\begin{bmatrix} > 0 & \cdot \\ > 0 & > 0 \end{bmatrix}$
C'	$\begin{bmatrix} > 0 & \cdot & \cdot & \cdot \\ < 0 & > 0 & \cdot & \cdot \\ > 0 & < 0 & > 0 & \cdot \\ < 0 & > 0 & < 0 & > 0 \end{bmatrix}$	$\begin{bmatrix} > 0 & \cdot \\ > 0 & > 0 \end{bmatrix}$
D'	$\begin{bmatrix} \sim 0 & \cdot & \cdot & \cdot \\ 0 & 0 & \cdot & \cdot \\ 0 & 0 & \sim 0 & \cdot \\ 0 & 0 & 0 & 0 \end{bmatrix}$	$\begin{bmatrix} \gg 0 & \cdot \\ > 0 & \gg 0 \end{bmatrix}$

Figure 4. Some hypothetical examples of the links between the phenotype for trait *y* and the oikotype of habitat feature *h*, and their corresponding variance-covariance matrices obtained from the MDHGLM (A', B', C', D'). Each ellipse represents a set of phenotypic-oikotypic values shown by one of the five individuals (genotypes). a) Individuals are not plastic and there is oikotypic variation (i.e., specialists). All individuals differ consistently in their mean phenotype and oikotype, and there is a positive among-individual correlation between phenotype and oikotype; b) Individuals differ consistently in their mean phenotype and their mean oikotype, but also plastically adjust their phenotype equally in response to the change in the oikotype they use; c) Individuals differ consistently in their mean phenotype and their mean oikotype. They also show different distributions of their oikotype and phenotypic plasticity. Specialists are less plastic and show high phenotypic and oikotypic values, while generalists are more plastic and show lower phenotypic and oikotypic values on average; d) Individuals are generalists that can use most of the full range of oikotypes available for the population and all display a plastic response to the oikotype they use.

Supplementary material Appendix 1

In the paper, we discuss a range of different modelling techniques. Here we give a brief introduction to each to help provide a little more background. G Artificial Intelligence (ChatGPT) was used for certain aspects of these descriptors. See also Figure 3 in the main text.

1. Generalized Linear Mixed Model (GLMM) - Figure 3a

Description:

A GLMM extends the general linear model (GLM) by including both *fixed effects* (parameters associated with an entire population) and *random effects* (parameters that vary across clusters or individuals).

Use case:

Commonly used for hierarchical or repeated-measures data, such as modeling animal counts, disease incidence, or behavioral data.

2. Multivariate GLMM (MGLMM) - Figure 3b

Description:

The MGLMM extends the GLMM to simultaneously model multiple response variables. It accounts for correlations both within and between responses.

Use case:

Useful in ecological or medical studies where several outcomes are measured on the same subjects (e.g., body condition and reproductive success).

3. Double Hierarchical Generalized Linear Model (DHGLM) - Figure 3c

Description:

A DHGLM extends the GLMM by modeling *dispersion* or *variance* as a function of both

fixed and random effects. That means both the mean and the variance can be modeled using random effects and predictors.

Use case:

Applied when data show heteroscedasticity (non-constant variance) or overdispersion — common in ecological and genetic studies.

4. Multivariate DHGLM (MDHGLM) - Figure 3d

Description:

The MDHGLMM combines the multivariate structure of MGLMMs with the double-hierarchical approach of DHGLMs. It allows both the mean and dispersion of multiple responses to depend on covariates and random effects while estimating the covariance among the multiple responses.

Use case:

Used for complex datasets with multiple interrelated responses showing variable dispersion, such as multi-trait animal breeding or environmental monitoring.

5. Causal Structure Mixed Model (CSMM) - see R code for an example

Description:

A CSMM incorporates causal relationships among variables directly into the mixed model framework. It can incorporate GLMMs or DHGLMS. It combines the strengths of multivariate mixed models with causal inference principles.

Use case:

Applied when the researcher aims to infer causal pathways rather than just associations — for example, determining how habitat quality *causes* changes in species abundance.

6. Resource Selection Functions (RSF) / Habitat Selection Models - example not given in

paper but discussed in Box 4.

Description:

RSFs (Box 4) or habitat selection models estimate the probability of an animal using a particular resource or habitat relative to its availability. Typically, they use logistic regression or GLMM frameworks, with used versus unused as the response

Use case:

Used in wildlife ecology to understand species–habitat relationships and predict habitat suitability.

Supplementary material Appendix 2

For the case study we present in box 2, after trying to catch selkies we simulated the data instead. The code to simulate the data, the data and annotated code to run the model are available on OSF (https://osf.io/n95ws/ ; DOI: 10.17605/OSF.IO/N95WS and github (https://github.com/JulienGAMartin/phenotype_oikotype_covariation) using this code. Actual data used in our case study can be found below this code. The parameters of the simulation can easily be modified to examine different data structures and biological questions.