Trait shifts during range expansions: A meta-analysis

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Abstract

Populations undergoing range expansions often undergo phenotypic shifts at the leading edge. Understanding how traits change during range expansions could provide insight into predicting invasive species dynamics and responses to climate change. Theory predicts that edge populations should increase in dispersal capability and shift towards reproductive traits that maximize fecundity over individual offspring investment. I conducted a quantitative synthesis of previously published research across a variety of plant and animal taxa to test whether core-to-edge changes in trait means and variance follow these theoretical predictions. While most variation in core-edge shifts was explained by within-study effect (corresponding to high heterogeneity among traits), populations showed a significant increase in dispersal-related traits. There were marginal increases in r-selected reproductive strategies and environmental tolerances, both coupled with a marginal reduction in phenotypic variance. Other trait groups showed no consistent core-edge changes in mean or variance. These results show that trait shifts generally follow the expectations of range expansion theory and highlight the importance of considering changes in trait distributions instead of just mean shifts.

Introduction

The dramatic environmental changes of the Anthropocene are driving range shifts in a wide in a variety of ecological contexts. Populations that are sensitive to novel climatic conditions are expected to adjust their distributions towards higher altitudes or latitudes in an effort to remain in a similar niche space (Chen et al., 2011), while invasive species are notorious for their ability to rapidly spread across new environments. Both during and after an expansion, individuals at the leading edge experience novel ecological and evolutionary pressures, which can favor trait shifts away from core phenotypes (Chuang & Peterson, 2016). These trait changes can alter the dynamics of an expansion and affect its overall outcome.

Range expansions are by driven a combination of migration from established populations towards the margin and reproduction in newly settled areas, while they can be slowed by increased edge mortality (Gaston, 2009; Skellam, 1951). Each of these forces can create selection pressures on edge phenotypes. During sufficiently long expansions, extrinsic conditions such as environmental gradients and community composition are likely to change over space, creating variation in the optimal trait values over the species range. At an equilibrium state, the distribution of phenotypes across the range is expected to be driven by the balance of directional selection towards these trait optima and migration from areas with different optima (Kirkpatrick & Barton, 1997; Shirani & Miller, 2022); however, active range expansions are inherently non-equilibrium processes and can support ephemeral phenotypic states that would be disadvantageous in static populations (Burton et al., 2010). In particular, expansions should favor traits that increase the rate of expansion or that are adapted to transitory edge demographic conditions.

Theoretical models of expanding populations typically assume a population density gradient that runs from high at the core to low at the edge (Phillips et al., 2010). These abundant center distributions were historically predicted to be a common feature of static range edges (Brown, 1984), although empirical research has not supported this as a general trend (Dallas et al., 2017; Sagarin & Gaines, 2002). However, active range shifts must have lower edge abundance for a least a brief window, which can lead to changes in optimal life history trade-offs (Burton et al., 2010). In general, high density core populations experience greater intraspecific competition and can be more enticing or familiar to predators; traits that maximize survival, improve resource efficiency, or otherwise minimize negative density-dependence (i.e., "K-selected" strategies) are beneficial under these conditions even if they are energetically expensive or come with restrictive trade-offs. Edge populations are often released from demographic pressures; instead traits that maximize reproductive rates (i.e., "live fast, die young" or "r-selected" strategies) are more advantageous (Reznick et al., 2002). For example, round gobies (*Neogobius melanostomus*) have a lower age of maturity and higher reproductive output at their population margin (Gutowsky & Fox, 2012), while dainty damselflies (*Coenagrion scitulum*) reduce investment in pesticide resistance (Dinh et al., 2016) and western bluebirds (*Sialia mexicana*) demonstrate less cooperation and sociality at the range front (Duckworth, 2006).

Phenotypic shifts can also interact with the expansion process itself, particularly for disperal-related traits. Individuals that move past the current population front are often able to take advantage of the benefits of low population density (Bowler & Benton, 2005). This can lead to spatial sorting that drives the evolution of increased dispersal rate, distance, or ability throughout the course of an expansion (Shine et al., 2011). The canonical example of this is the evolution of cane toad (*Rhinella marina*) limb length in Australia: each generation, toads with the longer legs could disperse farther and would define the new range limit. These would reproduce with each other, producing offspring with longer legs than the population average and ultimately leading to an accelerating invasion front (Phillips et al., 2010). Dispersal ability has also evolved in edge populations of bush crickets [*Conocephalus discolor*; Simmons & Thomas (2004)], speckled wood butterflies [*Pararge aegeria*; Hill et al. (1999)], and climbing hemp vines [*Mikania micrantha*; Huang et al. (2015)]. The evolution of dispersal-related traits is expected to be a particularly ephemeral characteristic of a shifting population, since their extraordinary fitness benefits dissipate when the range margin moves beyond the ability of dispersers to track.

Although much empirical and theoretical work has focused on the feedbacks between trait shifts and range expansion, phenotypic and genetic variation can also drive, limit, and respond to changing ranges. In static ranges, variation in fitness-related traits is expected to be lower at the margin than the center; however, multiple processes can drive variation changes during an active expansion, leading to different ephemeral patterns. Allele surfing (Slatkin & Excoffier, 2012), where a repeated cycle of edge colonization and rapid population growth creates a series of bottlenecks, can substantially restrict genetic diversity through a process that is spatially equivalent to genetic drift. Alternatively, if trait optima vary spatially, then the asymmetric gene flow driven by core-to-edge migration can increase trait variance by introducing non-adapted phenotypes (Bridle et al., 2009). Spatial sorting can also impact variation; for example, experimental invasions of *Callosobruchus* beetles yield increases in the phenotypic and genetic variance of dispersal distance (Ochocki & Miller, 2017). Processes affecting the spatiotemporal structure of trait variation during range expansions can ultimately limit trait mean evolution and help regulate the formation of stable boundaries (Takahashi et al., 2016).

Although the dynamics of trait shifts during range range expansions have attracted a broad research interest, the empirical evidence remains as a collection of case studies. In this study, I used meta-analysis to create a quantitative synthesis investigating changes in trait means and variance between core and edge populations. Specifically, I examined how consistently trait shifts in expanding populations follow theoretical predictions. I expected increases in dispersal ability and shifts towards higher reproductive rates at the edge, since these traits should be under the most direct and unambiguous selection pressures.

Materials and Methods

Literature Search

I searched Web of Science (Clarivate) for journal articles that matched search #5 in Table S1 on June 6, 2022 and supplemented these records with papers that cited or were cited by Chuang & Peterson (2016). I initially skimmed the titles and abstracts of the results to remove completely irrelevant records, then examined the remaining papers for three search criteria. Studies were considered for inclusion if they A) measured at least one phenotypic trait in B) populations that are currently undergoing range expansion and C) defined discrete core and edge or a continuous core-to-edge measure (e.g., distance from core, time since edge arrival). Papers that met these criteria were included if they contained enough information to calculate effect sizes (full datasets or summary statistics equivalent to means, standard deviations, and sample sizes).

The initial literature search returned 436 records, which I supplemented by an 126 additional papers. 166 papers passed the initial screening, 88 of which met all three selection criteria and 44 of which had usable data. The literature search produced 32 of the selected papers, while 12 came from the supplemental search. In total, I included 355 core-edge contrasts, covering 27 species (Table 1). I excluded binomial traits from the variation analysis, since their variance is a direct function of their mean; this resulted in a subset of 263 contrasts from 31 studies covering 19 species.

Data extraction and trait classification

From each study, means, standard deviations, and sample sizes were extracted for as many traits and populations as possible. If studies reported trait values by sex, species, transect, or some other grouping factor, these were extracted separately. Summary statistics only available in figures were extracted with custom R scripts (R Core Team, 2020); mean and standard deviations of data extracted from box plots were estimated with the estmeansd package (McGrath et al., 2020). Summary statistics were grouped into contrasts, the smallest units that contained a specific core-edge contrast or gradient (for example, a study with three edge and three core populations would form one contrast, while a study with three core-edge pairs would form three contrasts).

Given the breadth of the data in this analysis, the variety of phenotypes are challenging to consider together. Addressing this requires consistently handling both the magnitude and direction of trait shifts. I categorized each trait as behavior, body size, dispersal, energy (including energy acquisition, foraging, and metabolism), environmental tolerance, growth rate, or survival (including defense and immunity). Each trait was assigned a direction; traits predicted to increase at the edge were coded positive, while traits with predicted edge decreases were coded negative. Theoretical predictions are strong for several trait groups and were thus relatively easy to encode. For example, dispersal traits were generally positively encoded, as higher dispersal propensity and greater movement distances are expected to be more common on the edge. Traits that increased reproductive output or fecundity were assigned a positive direction, while individual reproductive investment (e.g., larger egg sizes) and age of maturity were encoded negatively. Traits associated with survival, defense, and immunity were assigned a negative code, as these are expected to be higher in high-density core populations. Bold, aggressive, or exploratory behaviors are expected at the edge and were positively encoded. Body size was tricky, as it tends to interact with multiple other traits that could be under selection during range expansions; for example, higher body size can be associated with a later age of maturity and better resistance to interspecific competition (core traits), but it could also be connected with increased fecundity and dispersal distance (edge traits). Ultimately, I coded larger body size as negative, although I do not expect consistent shifts in one direction or the other. As resource competition tends to increase in high-density populations, energy-associated traits were encoded negatively. Environmental tolerances were handled on a case-by-case basis, with traits expected to shift in the direction that was more adapted to the edge environment and encoded appropriately. All data-encoding decisions were made before analysis and without consideration of the associated data.

Effect Sizes

The location (core or edge) of each data point was standardized so that core and edge populations had measures of 0 and 1, respectively. For continuous measures of core-to-edge distance, the central 50% of the range was discarded and the remainder was discretized as core and edge.

To detect trait shifts (i.e., changes in means), means and standard errors were z-transformed with the weighted pooled standard deviation of each contrast. Binomial traits (e.g., number of individuals dispersing) were converted to proportions and standard errors, then logit transformed to be on z-scale. For measuring changes in variation from core to edge, I calculated each trait value's log-expected standard deviation and the associated error estimate:

$$\log \hat{\sigma} = \log s + \frac{1}{2(n-1)};\ SE[\log \hat{\sigma}] = \frac{1}{2(n-1)}$$

where s is the sample standard deviation and n is the sample size (Nakagawa et al., 2015).

Meta-Analysis

To examine whether traits shift in predictable directions during range expansions, I used a Bayesian hierarchical model $z_i \sim \alpha_i + \Delta_i x_i$, in which the standardized mean trait value (z-score) is the response and the primary predictor x_i is edge status (1 or 0) times trait direction (1 or -1). Conceptually, this is a random slopes model combined with a meta-analysis. I used a normal likelihood, with z_i distributed around its known standard error. The parameters α_i and Δ_i represent the z-score at the core and the core-to-edge change, respectively; variation within both parameters was partitioned into components for trait category, species, study, and contrast. Partial pooling (e.g., random effects) was used for variation in α_i and Δ_i because it allows for different categories to share some information when pertinent.

Publication bias was assessed by including the term $(1/n_i)(\gamma_i + \eta_i x_i)$ in the model, where n_i is the sample size (as per Nakagawa et al. (2022)). The two parameters account for the effects of sample size on the core (γ_i) and the edge effect (η_i); when sample size is large, the influence of γ_i and η_i on the model approach zero. Both publication bias parameters were allowed to vary by trait category and partially pooled. I compared the trait shift model with and without the publication bias component using K-fold cross validation. The data were partitioned into 11 folds of 4 studies; studies were randomly assigned to a fold under the constraint that no fold contained all of the data for a single trait type. For each fold, the model was re-run with the 4 studies excluded from the dataset (training), and the z-scores of the held out studies were predicted (testing). The expected log predictive density (ELPD) of each model was used to estimate model weights and perform model averaging through posterior predictive stacking (Yao et al., 2018).

Changes in variance were assessed with a similar random slopes model, based on Nakagawa et al. (2015): $\log \hat{\sigma}_i \sim \alpha_i + \Delta_i x_i + \beta \log y_i$, where y_i is the trait sample mean, β is a scaling factor that controls for mean-variance relationships, and α_i and Δ_i have the same interpretation and variance components as in the mean model. In both models, the estimating Δ_i and its components are the key to addressing the research objectives.

Prior distributions were weakly informative, with Normal(0,3) for the intercept and fixed effect coefficients and folded Student-$t_7^+(0, 3)$ distributions for the random effect standard deviations. These were selected to place low prior probability on regions of parameter space that are outside the bounds of reasonable inference (e.g., given that the data are on z-score scales, coefficients larger than 3 are quite unlikely) while adding light regularization within this range (Lemoine, 2019). Fixed effect coefficients (β and the baseline values of Δ, γ, and η) were given Normal(0, 1.5) priors, and the intercept (baseline α) was assigned a Normal(0, 3) prior. Correlation between random effects was modeled with a lightly-regularizing LKJ(2) prior (Lewandowski et al., 2009). Trait and variance changes were were considered significant if their 95% credible intervals excluded zero (e.g., zero is less than the 2.5% posterior quantile or greater than the 97.5% posterior quantile); changes were considered marginal if their 50% credible intervals excluded zero (based on 25% and 75% posterior quantiles, meaning that at least 75% of the posterior probability is on one side of zero).

All models were fit in R v. 4.2.0 with the brms package [v. 2.17.0; Burkner (2017)] using the cmdstanr backend with Stan v 2.30.1 (Carpenter et al., 2017). The primary models were run for 16 chains with 1200 warmup and 500 post-warmup iterations each on the Lonestar6 supercomputer at the Texas Advanced Computing Center. During cross-validation, models were re-run with only 8 chains to save on computational resources; model comparison was performed with the loo package. For all analyses, model convergence was assessed by ensuring all $\hat{R} < 1.01$, all bulk and tail $N_{eff} > 1000$, and no divergent transition or BFMI errors were reported.

Results

We used a Bayesian random slopes meta-analysis to assess core-edge trait shifts in expanding populations. In general, shifts in trait means varied substantially among different trait types (Figure 1, the large bars below the horizontal lines). In this analysis, traits were standardized so that traits predicted by theory to increase at the edge are coded as positive, while those predicted to increase in the core are coded negative (see methods). Dispersal traits shifted significantly towards higher dispersal ability at the edge ($\Delta = 0.342$ [95% Credible Interval: 0.079, 0.595]). Reproductive traits also became marginally more r-selective ($\Delta = 0.202$ [50% CI: 0.117, 0.287]), although the 95% credible interval did not exclude zero. Environmental tolerance ($\Delta = 0.174$ [50% CI 0.06, 0.287]) and body size ($\Delta = 0.096$ [50% CI: 0.019, 0.174]) also showed marginal shifts towards edge-expected phenotypes (smaller body size and local specialization, respectively). Behavior, energy, survival, and growth rate showed no evidence for consistent changes. Heterogeneity among core-edge contrasts was high (Figure 1, smaller bars). Several trait categories (body size, energy, reproduction) had mean-shift contrasts that were significantly different than zero in both directions, and all categories except for environmental tolerance included marginally increasing and marginally decreasing contrasts. These results are based on 355 trait shifts from 44 studies that measured traits from the core and edge of of range expansions; these covered 27 species across plants and animals (Table S1).

Changes in trait variation were less easily apparent (Figure 2), with no trait types showing significant phenotypic variance changes from core to edge (all 95% Credible Intervals include zero). However, variation in environmental tolerance (Δ = -0.123 [50% CI: -0.205, -0.017]) and reproduction (Δ = -0.085 [50% CI: -0.145, -0.022]) marginally decreased in edge populations. Change in variance results were based on a subset of 263 core-edge contrasts from 31 studies.

There was substantial effect heterogeneity for both mean and variance changes (Figure 3). Contrast-level variability (the within-study effect, the smallest unit of core-edge comparison) was dramatically greater than variation attributable to study, species, or trait type in both analyses, with among-study variation as the second largest component. Species-specific effects were negligible for both trait means and variances (Figure S1), and the overall amount of variation explained by trait type was lower in the variance model than the mean-shift model. Heterogenetiy among mean-shift contrasts was apparent across trait categories (Figure 1, smaller bars). Several trait categories (body size, energy, reproduction) had contrasts that were significantly different than zero in both directions, and all categories except for environmental tolerance included both marginally increasing and marginally decreasing contrasts. Most trait categories also had heterogenous changes in variation (Figure 2, smaller bars), although dispersal variability was consistently near zero among contrasts.

Publication bias was not a dominant factor in these results; I used cross validation to compare the baseline mean-shift model with a version made core-edge contrasts a function of reciprocal sample size and used to posterior predictive stacking to estimate the weights for each model. The model accounting for publication bias had a model weight of 7.7%, compared with a weight of 92.3% for the baseline model. Given this disparity, the values and figures presented here were from the baseline model.

Discussion

It is a common theme in evolution for species to arrive at different solutions to the same general problems. Given the taxonomic breadth of this meta-analysis and the unique ecological contexts of each range expansion, it is perhaps unsurprising that heterogeneity is so prevalent. Nevertheless, this analysis has identified a consistent shift towards improved dispersal capability of edge populations, which matches the extensive body of theory on spatial sorting (Cobben et al., 2015; Hargreaves & Eckert, 2014; Phillips & Perkins, 2019). Edge populations also tended towards reproductive strategies that maximize fecundity and showed tolerance of novel environments, although the evidence for these shifts was weaker than for dispersal. Both of these trait categories also showed edge reductions in phenotypic variance. Reduced phenotypic variance in these traits could lead to higher fitness via reduced genetic load if a greater portion of the population is near the optimal trait values. Finally, body size marginally decreased in edge populations; however, the effect size was small with a narrow credible interval, so caution is warranted in drawing conclusions.

The lack of significant or marginal shifts for traits related to behavior, survival, growth, or energy should not be interpreted as evidence that these traits not not change during a range expansion. Rather, these sorts of traits are more dependent on the ecological and evolutionary context, and can respond in heterogeneous ways. Variance changes in particular may depend on environmental contexts (Takahashi et al., 2016). A wide range of factors may contribute to the observed heterogeneity, including ephemeral effects, trait correlations, trade-offs, Allee effects, and expansion stochasticity.

While range expansions are dynamic processes, I was unable to address the temporal component in this meta-analysis. Dispersal traits are extremely beneficial during the initial colonization stage but can quickly become less optimal in a given location as the expansion front moves forward. This could lead to an ephemeral increase in dispersal capacity, followed by a subsequent decline (Burton et al., 2010). Fecundity-enhancing traits could produce a similar ephemeral pattern, though they may persist for longer than dispersal traits if the edge moves faster than the local population density approaches its carrying capacity. Shifts in environmental tolerance are likely to be more robust, as they involve adaptation to more stable conditions instead of transitory demographics. For each of these, trait differences between core and edge populations will depend not just on the relative distance (physical or temporal) between the locations but on the time since colonization of each.

Although the selective pressures on differing trait categories are usually considered independently, an emerging body of evidence suggests that trait correlations can play a significant part in the eco-evolutionary dynamics of range expansion. This covariation can arise from trade-offs between energetically costly edge traits (Chuang & Peterson, 2016) and may be facilitated by genetic architecture. In particular, species have shown trade-offs between dispersal and reproduction (Duckworth, 2006; Hughes et al., 2003; Simmons & Thomas, 2004) and between dispersal and immune function (Brown et al., 2007). Ochocki & Miller (2017) identified negative genetic correlations between dispersal and fecundity in experimental *Callosobruchus* beetle invasions and used theory to assess the impact of genetic structure on expansion outcomes: positive correlations can increase the stochasticity of an expansion, while negative correlations can result in more consistency but reduced trait shifts. Unfortunately, most of the studies that I was able to include in this meta-analysis did not examine trade-offs or trait correlations.

For some species, the assumptions of higher fitness at low edge density may be inaccurate. Marginal populations can suffer demographic Allee effects, where low population density decreases individual fitness (Stephens et al., 1999). This is often due to a breakdown in cooperative behavior or mate location (Courchamp et al., 1999; Wells et al., 1998), and it can alter the selective pressures on behavior, reproductive, and life history traits. In the presence of low individual edge fitness, the spread dynamics can shift from a pulled wave, in which expansion is driven almost solely by the vanguard, to a pushed wave, where dispersal from the intermediate demes contributes to both the edge and future expansion (Miller et al., 2020). Within pushed waves, K-selective reproductive strategies can have higher fitness, and the effects of spatial sorting may be reduced. Expansion type can also vary within species based on ecological context; for example, yeast populations expand with pushed waves when cooperation enhances resource extraction, but use pulled waves in the absence of Allee effects (Gandhi et al., 2016). Environmental restrictions or interspecific interactions that reduce edge fitness can also create a pushed wave dynamic. The cane toad parasite *Rhabdias pseudosphaerocephala*, which is expanding its edge slightly behind its host's invasion front, shows larger egg mass, greater body size, and higher individual survival rates in edge populations (Kelehear et al., 2012). These shifts are more characteristic of a pushed wave; they are beneficial at the edge because cane toad density is lower, so increased survival raises the chance of encountering a potential host more than increased fecundity. The higher gene flow from the core can also increase genetic and trait variation in a pushed wave.

Finally, the degree of among- and within-study heterogeneity in my results could be partially explained by the inherent stochasticity of range expansions (Phillips, 2015). Even if selection for edge-specific phenotypes is strong, low population density can exacerbate the effects of allele surfing. This could potentially accelerate alleles that enhance dispersal and demographic traits (Gralka et al., 2016) or fix disadvantageous mutations, producing edges traits that are quantitatively and qualitatively different from the optima (Peischl et al., 2015). As such, the trait shifts included in this meta-analysis could be best viewed as realizations from a wider distribution of trait changes that could potentially have different outcomes if the expansion were to have happened again. Interestingly, experimental results have shown that the degree of stochasticity seems to vary among taxa (Miller et al., 2020). Several beetle expansion experiments found substantial among-replicate variance in edge-shifts of dispersal and reproductive traits (Ochocki & Miller, 2017; Szűcs et al., 2017; Weiss-Lehman et al., 2017). Conversely, experiments with *Arabidopsis* found that edge populations were more predictable when evolution is possible (Williams et al., 2016). Williams et al. (2019) suggests that reproductive systems or life history strategies that increase genetic variation in edge populations should reduce expansion stochasticity; in particular, pushed expansions should make trait shifts more deterministic. Developing a better understanding of the factors that can contribute to this heterogeneity will be important to better predicting the outcomes of range expansions.

Given the ongoing ecological crises of climate change and biological invasions, range expansions will be increasingly common. Understanding the eco-evolutionary feedbacks involved will be critical for developing effective forecasting and management methods. While the general increase in edge dispersal is supported across a variety of taxa, other trait shifts are not as easily predicted. Future research should focus on the factors that contribute to such disparate evolutionary outcomes. In particular, considering trade-offs and correlation between different fitness-related traits should be increasingly prioritized during expansions. While the emerging trend of experimental invasions has provided greater mechanistic detail on trait evolution during expansion, these studies have generally been limited to a small number of model species with short generation times (Miller et al., 2020), which may not generalize well to the taxonomic breadth of *in situ* expansions. Investigating species with multiple, separate invasions could provide insight into resolving expansion stochasticity within natural environments. Finally, explicitly considering trait variance will provide a more complete understanding of edge evolutionary ecology; although assessing genetic variance is not always a logistically or financially viable option in field studies, changes in phenotypic trait variation should be relatively straightforward to incorporate.

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Figures

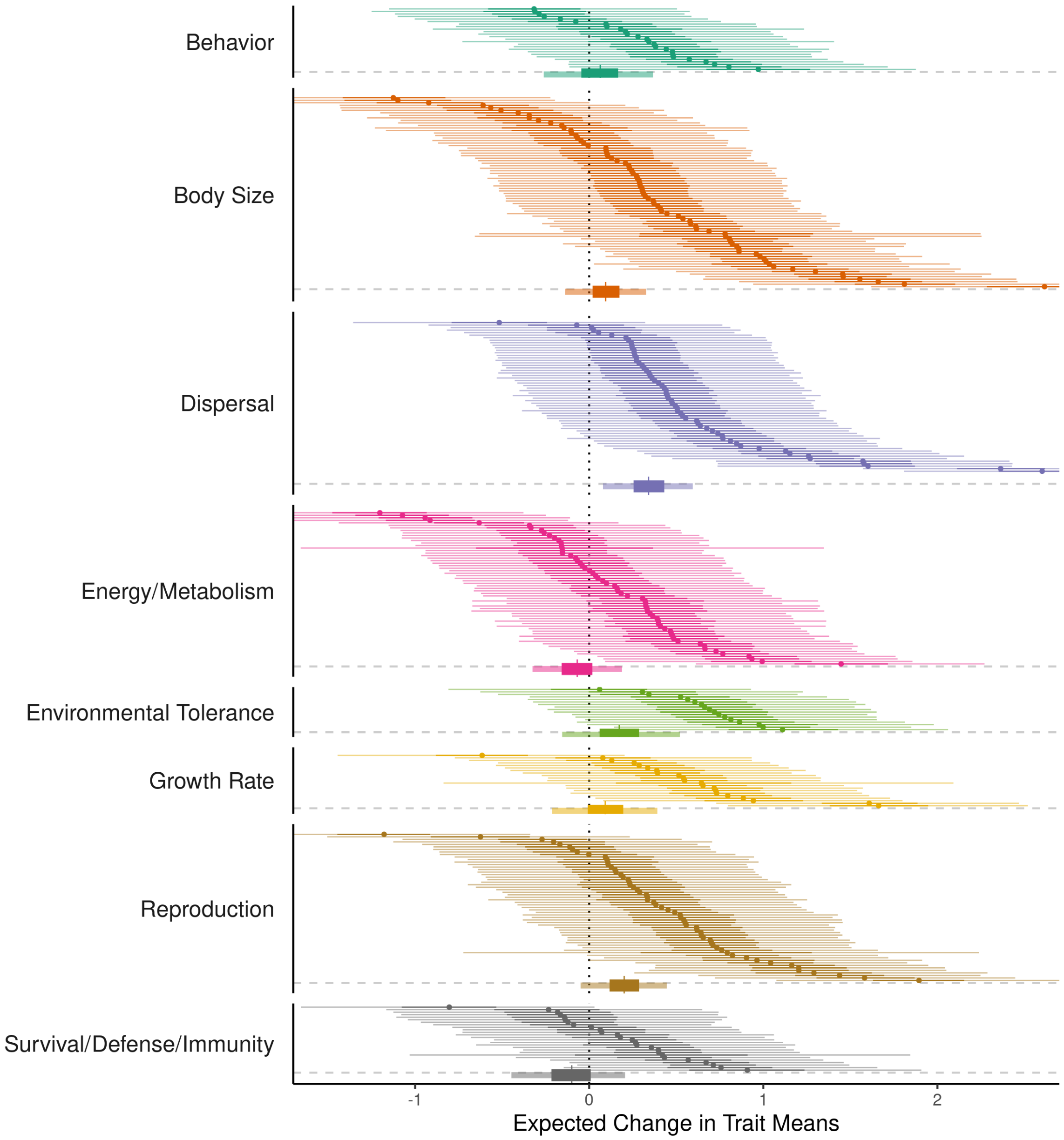

Figure 1: Changes in trait means from core to edge. Positive values indicate trait changes the predictions of theory. Model estimates for each core:edge contrast are show above the dashed lines (N = 355); estimated conditional mean shift for each trait category is below. Both statistics are shown with the median, 50%, and 95% credible intervals of the posterior distribution; differences are considered significant if the 95% credible interval excludes zero.

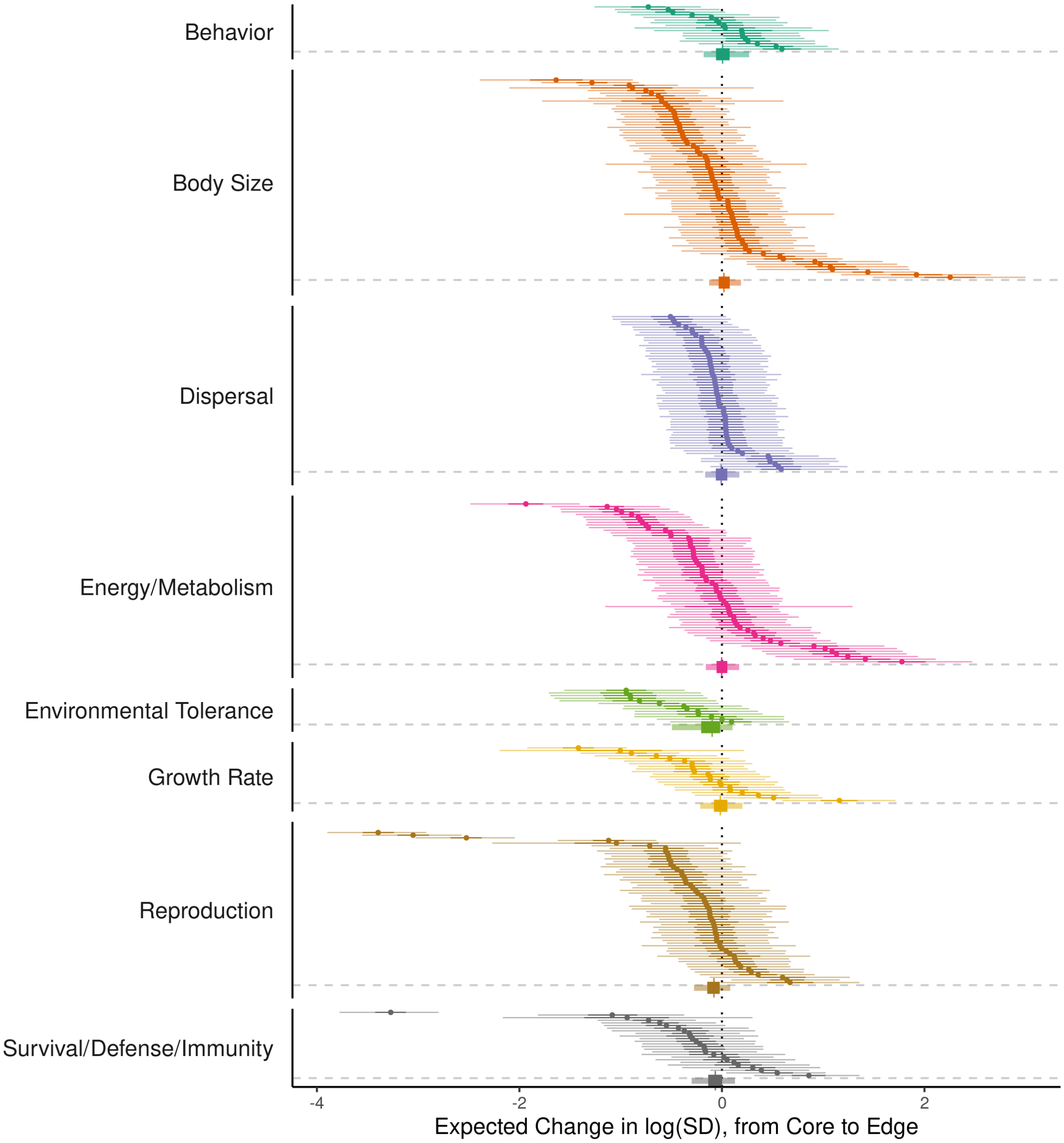

Figure 2: Changes in trait variation from core to edge. The posterior change for each core:edge contrast are show above the dashed lines (N = 263), while conditional mean changes for each trait category are below. Both statistics are shown with the median, 50%, and 95% credible intervals of the posterior distribution; differences are considered significant if the 95% credible interval excludes zero.

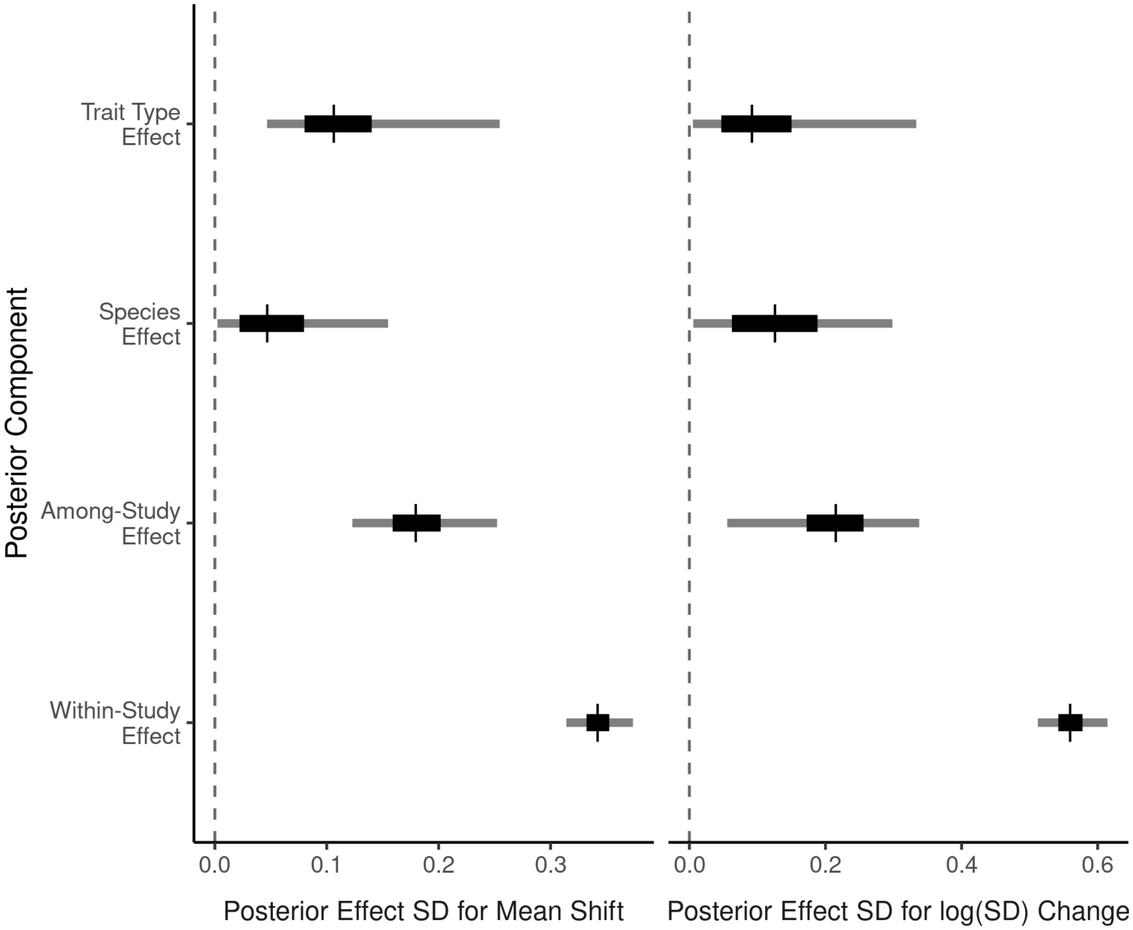

Figure 3: Variation among effect categories for mean (left) and variance (right) models. Values are the standard deviation of the category's random effects for the core-edge change, with the median, 50%, and 95% credible intervals of the posterior distributions.

Tables

Table 1: Data sources, organized by species. The number of core-edge contrasts from each trait category is also presented.

Species	Source	Behavior	Body Size	Dispersal	Energy/ Metabolism	Environ-mental Tolerance	Growth Rate	Repro-duction	Survival/ Defense/ Immunity
Acridotheres tristis	Magory Cohen et al. (2020)	4							
Aegilops triuncialis	Rice et al. (2013)		6						4
Aratus pisonii	Johnston & Smith (2018)		1						1
Aratus pisonii	Riley & Griffen (2017)							5	
Argiope bruennichi	Wolz et al. (2020)		1					2	
Calopteryx splendens	Hassall et al. (2009)			6					
Coenagrion scitulum	Dinh et al. (2016)			12	12			24	3
Coenagrion scitulum	Therry, Lefevre, et al. (2014)	10					2		
Coenagrion scitulum	Therry, Gyulavári, et al. (2014)		4	12	4				
Coenagrion scitulum	Therry, Zawal, et al. (2014)		3	12	3				3
Coenagrion scitulum	Therry et al. (2015)		5	5				15	
Coregonus albula	Amundsen et al. (2012)		10				5	5	5

Species	Source	Behavior	Body Size	Dispersal	Energy/ Metabolism	Environ-mental Tolerance	Growth Rate	Repro-duction	Survival/ Defense/ Immunity
Crocothemis erythraea	Raffard et al. (2020)	1	2	1					2
Gladiolus gueinzii	Tabassum & Leishman (2018)			14	14		7	7	
Harmonia axyridis	Lombaert et al. (2014)		4	2					
Hemichromis letourneuxi	Lopez et al. (2012)	2		1	2			1	
Hypophthalmicthys molitrix	Tucker et al. (2020)		8					3	
Ischnura elegans	Carbonell & Stoks (2020)				4	4	8	3	4
Ischnura graellsii	Swaegers et al. (2022)		2		8	8	2	2	
Linepithema humile	Abril et al. (2013)			1	1			2	
Megacopta cribraria	Lovejoy & Lozier (2021)		22	22					
Merizodus soledadinus	Laparie et al. (2013)		4	6	4			2	
Mikania micrantha	Huang et al. (2015)			1				1	
Neogobius melanostomus	Gutowsky & Fox (2011)		4						
Neogobius melanostomus	Gutowsky & Fox (2012)						2		
Pacifastacus leniusculus	Hudina et al. (2015)	3							

Species	Source	Behavior	Body Size	Dispersal	Energy/ Metabolism	Environmental Tolerance	Growth Rate	Reproduction	Survival/ Defense/ Immunity
Pacifastacus leniusculus	Rebrina et al. (2015)				10			2	
Passer domesticus	Kilvitis et al. (2018)	2							
Passer domesticus	Kilvitis et al. (2019)								2
Passer domesticus	Martin et al. (2017)								5
Plantago lanceolata	Wan et al. (2018)				10				
Proterorhinus semilunaris	Grabowska et al. (2021)		8		2			3	
Rhabdias pseudosphaerocephala	Kelehear et al. (2012)		2		2			4	
Rhinella marina	Gruber et al. (2017b)	4		4					
Rhinella marina	Gruber et al. (2017a)	4							
Rhinella marina	Llewelyn et al. (2010)		4	4					
Rhinella marina	Phillips (2009)						2		
Rhinella marina	Phillips et al. (2010)		1	1					
Rhinella marina	Pizzatto et al. (2017)	1		3					
Triadica sebifera	Park et al. (2012)					5		6	
Xenopus laevis	Courant et al. (2017)							6	

Species	Source	Behavior	Body Size	Dispersal	Energy/ Metabolism	Environmental Tolerance	Growth Rate	Reproduction	Survival/ Defense/ Immunity
Xenopus laevis	Courant, Adil, et al. (2019)		2				2		
Xenopus laevis	Courant, Secondi, et al. (2019)		2	8					
Xenopus laevis	Louppe et al. (2018)		4		8				

Supporting Information

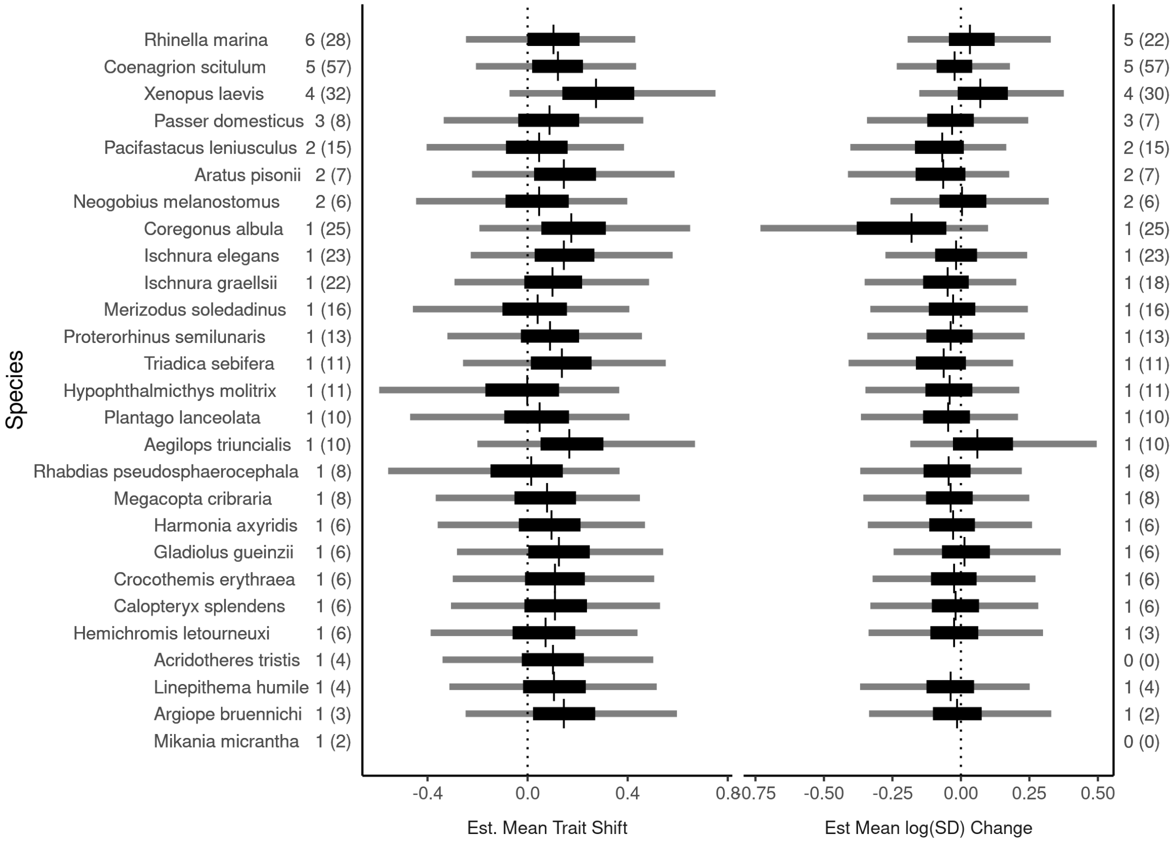

Figure S1: Species effects on changes in trait means and variances from core to edge, with posterior median, 50%, and 95% credible intervals. Numbers along the axes indicate the number of studies and number of effect sizes (in parentheses) the species contributed to in the mean dataset (left) and the variance dataset (right).

Table S1: Web of Science terms used in literature search. The first four search terms were used to filter potential papers along different axes; these were combined into search five, which was used to select the initial set of papers.

ID	Search terms
#1	SU=("Biodiversity & Conservation" OR "Entomology" OR "Environmental Sciences & Ecology" OR "Evolutionary Biology" OR "Life Sciences Biomedicine Other Topics" OR "Marine & Freshwater Biology" OR "Physiology" OR "Plant Sciences" OR "Zoology") AND PT=J
#2	TS = ((range NEAR (edge OR shift OR margin OR expanding OR expansion)) OR (population NEAR edge_terms))
#3	TS = (core OR center)
#4	TS = (trait$ OR phenotype$)
#5	#1 AND #2 AND #3 AND #4