Reconstructing Ecological Niche Evolution When Niches Are Incompletely Characterized

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Abstract

Evolutionary dynamics of abiotic ecological niches across phylogenetic history can shed light on large-scale biogeographic patterns, macroevolutionary rate shifts, and the relative ability of lineages to respond to global change. An unresolved question is how best to represent and reconstruct evolution of these complex traits at coarse spatial scales through time. Studies have approached this question by integrating phylogenetic comparative methods with niche estimates inferred from correlative and other models. However, methods for estimating niches often produce incomplete characterizations, as they are inferred from present-day distributions that may be limited in full expression of the fundamental ecological niche by biotic interactions,

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dispersal limitations, and the existing set of environmental conditions. Here, we test whether incomplete niche characterizations inherent in most estimates of species' niches bias phylogenetic reconstructions of niche evolution, using simulations of virtual species with known niches. Results establish that incompletely-characterized niches inflate estimates of evolutionary change and lead to error in ancestral state reconstructions. Our analyses also provide a potential mechanism to explain the frequent observation that maximum thermal tolerances are more conserved than minimum thermal tolerances: populations and species experience more spatial variation in minimum temperature than in maximum temperature across their distributions, and consequently may experience stronger diversifying selection for cold tolerance.

Key words: phylogeny, ecological niche, bias, rates of evolution

Introduction

Fundamental abiotic ecological niches are seen as reflecting physiological requirements scaled and translated to coarse spatial and temporal scales, with respect to static, non-interactive variables such as climate (Peterson et al. 2011). As such, they constitute a stable, long-term constraint on the distributional potential of the species. Lineages that retain abiotic ecological niche requirements over time will exhibit strong statistical dependence among trait values as related to their phylogenetic relationships (phylogenetic signal; (Revell et al. 2008) This pattern is usually referred to as phylogenetic niche conservatism (PNC) (Harvey and Pagel 1991). Disagreement exists with regard to how PNC should be defined, with some arguing that PNC can be invoked only if species diverge less in their abiotic niche requirements than expected under a random stochastic process, (Losos 2008, Revell et al. 2008); here, we use a minimalist definition of PNC as detectable phylogenetic correlation of abiotic niche parameters.

PNC has received considerable attention in recent years (Ackerly et al. 2006, Eaton et al. 2008, Diniz-Filho et al. 2010, Kozak and Wiens 2010a, Cooper et al. 2011, Nyári and Reddy 2013, Khaliq et al. 2015, Pyron et al. 2015, Strubbe et al. 2015). This attention comes because PNC can partly explain a broad array of ecological and biological phenomena, including geographic modes of speciation (Graham et al. 2004, Wiens et al. 2010) and latitudinal diversity gradients (Diniz-Filho et al. 2007, Hawkins et al. 2007, Rangel et al. 2007, Pyron and Burbrink 2009, Romdal et al. 2013). Assumptions of niche conservatism are also inherent, whether stated explicitly or not, in studies that use ecological niche modeling to predict the fate of biodiversity under future climate change scenarios (Peterson et al. 2002, Saupe et al. 2011, Quintero and Wiens 2013, Saupe et al. 2014) and to estimate past distributional dynamics in conjunction with phylogeographic studies (Nogués-Bravo 2009, Alvarado-Serrano and Knowles 2014, Dellicour et al. 2014, Hosner et al. 2014, Planas et al. 2014).

Tests and analyses of PNC, however, are complicated by the difficulty of estimating the full suite of abiotic conditions under which a species is able to maintain stable populations (i.e., the fundamental ecological niche) (Peterson et al. 2011). Mechanistic studies offer a means to obtain complete abiotic niche estimates in theory, but these studies are time-consuming, expensive, and often impossible to implement for many organisms or in many environmental dimensions. Furthermore, they often require detailed and unavailable estimates of many parameters, and involve lab scenarios that do not transfer appropriately to real-world conditions (Peterson et al. 2015). For non-model organisms, abiotic niche requirements are generally inferred from correlative ecological niche models (ENMs) that relate a species' occurrences to environmental data layers to derive a set of empirical associations (Elith et al. 2011, Peterson et al. 2011), or are estimated directly as the set of environments corresponding to known

occurrences (Ackerly et al. 2006, Kozak and Wiens 2010b, a). Using niches quantified from ENMs is an intriguing solution, because niches can be estimated for virtually any organism for which adequate occurrence and environmental data exist, creating possibilities to examine large and diverse lineages for meaningful phylogenetic comparisons (Godsoe 2010a).

Unfortunately, empirical estimates of ecological niches will most often comprise a subset of the full range of conditions in which a species can persist, because species' geographic distributions represent the intersection of three sets of constraints. First, areas that present habitable abiotic conditions for long-term population stability fall within the set of environmental conditions referred to as the fundamental niche that are of interest to characterize for PNC. However, frequently, only a subset of the full suite of conditions a species can tolerate will be represented across the globe (Godsoe 2010a). Second, this set of conditions will be reduced further by areas that are accessible via dispersal, because many otherwise-favorable areas of the globe will be unoccupied because they are separated from occupied habitat by biogeographic barriers (Godsoe 2010b). Third, areas may exist that are environmentally favorable but are unoccupied because of the absence of necessary biotic components (Afkhami et al. 2014) or because of negative biotic interactions. Therefore, the occupied set of conditions often represents a subset of the true fundamental niche due to the effects of "existing" abiotic condition, dispersal constraints, and biotic interactions (Soberón 2007, Peterson et al. 2011), such that any niche characterization that relies on it will be incomplete (Saupe et al. 2012, Owens et al. 2013). This reduced set of environmental conditions associated with a species' distribution, after effects of access and interactions with other species, is referred to as its realized abiotic niche (Soberón 2007).

Here, we build on previous work that explored approaches and underlying assumptions

involved in measuring PNC (Revell et al. 2008, Warren et al. 2008, Cooper et al. 2010, Godsoe 2010b, Wiens et al. 2010, Broennimann et al. 2012, Crisp and Cook 2012, Warren et al. 2014, Münkemüller et al. 2015) to examine effects of mapping incompletely characterized niches onto phylogenies. Specifically, we assess the influence of niche estimate truncation on niche evolution rate estimation using a novel simulation approach. By niche estimate truncation we refer to niches that are incompletely characterized as the result of deriving estimates from occupied areas, a practice which has been hypothesized to produce upwardly-biased estimates of rates of niche evolution, but which has not been assessed quantitatively (e.g., (Warren et al. 2008, Broennimann et al. 2012, Warren et al. 2014). We compare rates estimated from realized abiotic niche estimates to true rates derived from fundamental niches, providing a framework for understanding potential error in PNC analyses. Identification of error in PNC analyses is important for interpreting abiotic niche evolution patterns realistically across clades: only when patterns are correctly characterized can process be inferred, and then only with caution.

Methods

Evolutionary relationships

In order to base our simulations on a realistic evolutionary framework, we used the topology of a phylogeny inferred in a recent study of New World oriole species (genus *Icterus*) (Powell et al. 2014); we note that our analyses are general simulations, and have no connection to orioles, other than using their phylogenetic topology. We used the Bayesian maximum clade credibility tree from Powell et al. (2014), inferred from BEAST 1.7 (Drummond et al. 2012), based on mitochondrial and nuclear DNA sequences. We retained 32 tips in the analysis, pruning the tree to all currently-recognized oriole species except for *I. oberi* (Clements et al. 2016). This

well-resolved phylogeny was used to provide an empirically-relevant backbone topology and branch length structure on which to analyze niche evolution using virtual species, not to say something general or specific about orioles.

Virtual species

Several approaches have been used to characterize suitable abiotic niche conditions for comparative phylogenetic analysis, including the central tendencies of responses (Ackerly et al. 2006, Kozak and Wiens 2010b, a, Cooper et al. 2011), distributions of responses (Evans et al. 2009, Smith and Donoghue 2010), and minimum and maximum values of responses (Graham et al. 2004, Yesson and Culham 2006). Here, we focus on maximum and minimum tolerances of species, as they are likely features of abiotic ecological niches that are under selection, and the most sensitive to incomplete characterization. For simplicity, we assume that the range of temperatures at which a species is found is the direct result of evolutionary changes in thermal tolerances (Cooper et al. 2010).

To construct virtual species' niches, we simulated quantitative BM trait evolution on the phylogeny in the R package 'phytools' v.0.5-38 (Revell 2012). The BM model is commonly used to mimic the evolution of continuous characters (Felsenstein 1988), and is considered appropriate for evolutionary processes under genetic drift and some types of natural selection (Felsenstein 1988, O'Meara et al. 2006, Revell and Harmon 2008). To assess influences of environmental regime on niche truncation, we simulated warm-adapted and cold-adapted clades, with means of zero random normal changes along branches of the tree (Mu) and instantaneous variances (σ^2) of 300 (Fig. S1). For the warm-adapted clade, minimum temperature tolerances were simulated within the bounds of 0 to 20°C with a root node of 5°C, and maximum

temperature tolerances were simulated between 25 and 45°C with a root node of 27°C. For the cold-adapted clade, minimum temperature tolerances were simulated within the bounds of -23 to -3°C with a root node of -18°C, and maximum temperature tolerances were simulated between 8 and 28°C with a root node of 10°C. To characterize effects of incomplete estimates of abiotic niche, we generated 10 different estimates of upper and lower temperature bounds for each clade, producing a total of 20 simulated scenarios from which to assess abiotic niche evolution across the tree (hereafter referred to as niche scenarios). A total of 640 virtual species' thermal abiotic niches was generated, from the combination of 32 species x 10 niche scenarios x 2 adaptation scenarios (i.e., warm- versus cold-adapted clades).

Simulation framework

The geographic domain of our simulation was a 10'(~18 km at the Equator) grid of North and South America, projected to World Equidistant Conic. Maximum temperature of the warmest month (bioclim 5) and minimum temperature of the coldest month (bioclim 6) for the region were derived from WorldClim (Hijmans et al. 2005). We identified suitable environmental conditions across North and South America within each species' climatic envelope based on simulated upper and lower temperature limits (i.e. the species' thermal niche). A pixel was considered suitable if two conditions were met: bioclim 6 above the simulated lower temperature limit, and bioclim 5 below the simulated upper temperature limit.

Species rarely occupy the full extent of their potential suitable area: both biotic and dispersal constraints work to limit their distributions (Barve et al. 2011, Peterson et al. 2011). Thus, after identifying niches and potential distributions for each species, species' distributions were generated from within this area using a cellular automaton algorithm that considered

random dispersal processes and geographic barriers developed using the R packages ‘simecol’ v.0.8-9 (Petzoldt and Rinke 2007) and ‘raster’ v.2.5-8 (Hijmans 2016). Dispersal in this formulation follows Qiao et al. (2016), and represents the process of colonization and range expansion that would occur over many decades to centuries. First, 100 seeds were randomly placed within the species’ potential distributional area. From each of these initial seed points, the species dispersed stochastically within the suitable area, producing 100 different potential distributions. The dispersal distance was based on dispersal kernel limits, meant to replicate a range of dispersal capacity from poor to excellent, the latter corresponding to species’ ability to occupy the full extents of their potential distributions. Five maximum dispersal thresholds were used: 12, 25, 50, 100, and “all.” At the poor end of the dispersal spectrum, species could search at most 12 pixels, or ~220 km, whereas the most vagile species could reach the full extent of their potential suitable habitat. The maximum distance would vary, however, depending on the conformation of suitable habitat on the landscape. Searches were also limited by large-scale riverine and lake barriers from the ESRI waterbodies dataset; features wider than 10’ (e.g., Amazon, Mississippi, Paraguay, and Orinoco Rivers) were treated as hard limits to species’ dispersal. Of course, some of the barriers we used could be overcome by terrestrial organisms that fly or swim, but for the purposes of our study provide a realistic framework to place distributional limits on species in the absence of biotic factors that further constrain species’ ranges.

Once an occupied geographic distribution had been simulated, we extracted the maximum and minimum temperature from bioclim 5 and bioclim 6, respectively, from this distributional area. These values represented the estimated niche of the species, under an assumption of comprehensive sampling of environments across the species' geographic

distribution. We repeated the process for each species and dispersal replicate 100 times, for a total of 320,000 simulations: 32 virtual species x 100 simulated distributions x 20 niche scenarios x 5 dispersal abilities.

Niche evolution

We computed the rate of Brownian motion (BM) evolution (σ^2) using the 'fitContinuous' function in the R package 'geiger' v.2.0.6 (Harmon et al. 2008), to match the model used in the simulations. σ^2 is equal to the rate of variance accumulation per unit of branch length (Felsenstein 1985, O'Meara et al. 2006), and has been interpreted as a measure of the rate of ecological niche evolution (Cooper et al. 2011). Smaller σ^2 values can be interpreted as representing less niche evolution, and larger σ^2 values as more niche evolution when compared to each other. As mentioned previously, σ^2 itself does not provide information on whether niches are conserved, but rather information on the degree of PNC among traits or groups – in this case, a known σ^2 compared to σ^2 derived from distributional simulations (Revell et al. 2008, Cooper et al. 2011). We estimated σ^2 both with and without including standard error estimates. We allowed error to be estimated rather than inputting specific values, because we would rarely, if ever, know the true degree of error (i.e., niche truncation) in empirical data. σ^2 was calculated for the 20 'true' niche scenarios, and for each of the 10,000 runs simulating realized distributions from which to infer a given 'true' niche scenario (100 distributional replicates for each niche and dispersal scenario). All σ^2 estimates were log-transformed to conform to the assumption of normality, and we assessed whether and how these rates deviated from true rates using *z*-tests.

Environmental heterogeneity

To examine the potential influence of spatial heterogeneity of climate on rates of niche evolution, we assessed spatial variation in minimum and maximum temperature across North and South America in two ways. (i) We quantified variance on centered and standardized minimum and maximum temperatures associated with species' potential distributions under each evolutionary scenario. We provide an average variance across all species within a scenario, as patterns for individual species were similar. (ii) For each species and dispersal threshold, we examined the variance in maximum and minimum temperature values returned from the 100 distributional replicates. Patterns were similar across dispersal scenarios, so we provide averages across scenarios.

Results

Per-species mean minimum temperature truncation ranged 1–5°C as dispersal capacity decreased in cold-adapted clades. Niche truncation was less severe for maximum temperature tolerance, varying inversely with dispersal capacity from virtually none to 1°C (Fig. 1). These same patterns were observed in the warm-adapted clades, although the magnitude of per-species mean truncation was reduced compared to cold-adapted clades. Per-species average niche truncation for minimum and maximum temperature tolerances ranged 0–3°C and 0–1.5°C, respectively (Fig. 1).

Rates of niche evolution were significantly overestimated for minimum temperature tolerance under all dispersal thresholds except the 'full' category, in which all pixels were accessible (Table S1, Fig. 2, Figs. S2-S10). That is, when virtual species could search all of their potential distributional areas, rates of niche evolution did not differ significantly from true rates; this result held for both warm- and cold-adapted scenarios (Table S1, Figs. S5 & S10). In

general, rates of evolution for maximum temperature tolerance did not deviate significantly from true rates for either the warm- and cold-adapted scenarios under all dispersal scenarios (Table S1, Fig. 2, Figs. S2-S10). Although true rates of evolution for maximum and minimum temperature tolerances were simulated such that they did not differ significantly from each other, rates from realized abiotic niche simulations did diverge (Fig. 2, Figs. S2-S10). Estimated evolutionary rates for maximum temperature tolerance were significantly lower compared to minimum temperature tolerance for both the warm- and cold-adapted scenarios.

When potential error was included and estimated by the models, rates of evolution were significantly lower compared to true rates for all dispersal categories, except for the "full" threshold (Table S2). This result held for both maximum and minimum temperature tolerance, although more significantly so for the latter. Similar patterns were observed for both cold- and warm-adapted scenarios, although rates were depressed more substantially in the former (Fig. 3, Figs. S11-S19).

Minimum temperature tolerance is more heterogeneous across the landscape, regardless of the geographic focus of the analyses (i.e., North or South America). This result was consistent for both the analyses quantifying variance on centered and standardized minimum and maximum temperatures (Fig. 4), and for the analyses examining the variance in maximum and minimum temperature values returned from the 100 distributional replicates (Fig. 5).

Discussion

Our simulations provide quantitative support for the suggestion that rates of niche evolution are overestimated when niches are incompletely characterized (Warren et al. 2008, Godsoe 2010b, Broennimann et al. 2012, Warren et al. 2014). This observation is a recognized

instance of a more general problem in phylogenetic methods: unaccounted-for error in trait values upwardly biases estimates of the BM rate parameter σ^2 (Ives et al. 2007, Silvestro et al. 2015). Only when measurement error was minimal—in our case, only when species filled the full extent of their potential suitable area (Araújo and Pearson 2005)—did rates of niche evolution reconstructed by these methods mirror true rates. However, the prospect that all species in a clade can sample, let alone occupy, the full range of their existing fundamental niches is highly unlikely in real-world systems (Peterson 2003). Instead, biotic limitations (e.g., competition) and dispersal constraints will often prohibit species from attaining their full distributional potential, resulting in truncated abiotic niche estimates for at least some species in an analysis. We provide quantitative support that this truncation will make it appear as if more niche evolution has occurred within a clade than reality (Warren et al. 2008, Broennimann et al. 2012, Warren et al. 2014).

Skewed rate parameters will be particularly problematic for macroevolutionary studies comparing rates between or among clades, if species in these clades differ in their ability to disperse to and fully occupy their potential distributional areas (Warren et al. 2008, Broennimann et al. 2012). If two clades (A and B) are undergoing niche evolution at the same rate, but species in Clade A are more capable dispersers than species in Clade B, the rate of evolution for Clade A will appear lower than the rate of evolution for Clade B. The resulting interpretation of processes controlling niche evolution in these two groups would be in error. In this scenario, dispersal would appear as a causative agent in augmenting niche evolution, whereas in reality it is causative only of degree of what could be termed "niche expression."

Our simulations returned a greater variance in evolutionary rates for minimum temperature tolerance than for maximum temperature tolerance. This result likely owes to greater

heterogeneity in minimum temperature across the landscape, resulting in a greater degree of niche truncation (Fig. 1). Indeed, maximum temperature varied spatially to a much lower degree, which resulted in only occasional, and usually insignificant, underestimation of evolutionary rates. In these situations, realized abiotic niche values were similar across species, even though fundamental abiotic niches differed. Freckleton and Jetz (2009) and Warren et al. (2014) cautioned against a similar phenomenon, noting that spatial autocorrelation in environmental variables may cause closely-related species to share similar ecological traits solely because of dispersal limitation and a spatially-autocorrelated environment, even if true trait values for species actually diverge. This effect in turn would result in inaccurate estimates of phylogenetic dependence and potentially *dampened* estimates of rates of niche evolution.

Maximum temperature of the warmest month and minimum temperature of the coldest month are commonly used in PNC analyses (Peterson et al. 2011, Araújo et al. 2013) and do represent some degree of realism with respect to how maximum and minimum temperatures vary across landscapes. If these two variables reflect how temperature extremes fluctuate spatially, our result may explain, at least in part, why maximum temperature tolerances appear more conserved than minimum temperature tolerances (Cooper et al. 2011). That is, maximum temperatures are less variable across the landscape than minimum temperatures, which causes rates of evolution to appear lower for high temperatures. However, if tolerance to heat is indeed largely conserved, whereas tolerance to cold varies, as suggested by a recent study using mechanistically-determined thermal tolerances for terrestrial ectotherms, endotherms, and plant species (Araújo et al. 2013), then populations and species may experience stronger diversifying selection for cold tolerance because they experience more spatial variation in cold temperatures than in warm temperatures. Of course, more work needs to be done to confirm the validity,

generality, and applicability of this new hypothesis. Do similar patterns result when actual spatial and temporal variance in minimum and maximum temperatures are examined?

To account for truncation errors due to spatial heterogeneity and failure to recover the full extent of species' realized abiotic niches, we explored whether including measurement error would mitigate erroneous σ^2 estimates. However, this change often resulted in σ^2 values of niche characteristics being underestimated compared to true rates. Thus, whether one should incorporate estimated measurement error in analyses depends on the hypotheses and questions being asked. Incorporation of measurement error in our analyses did tend to minimize estimated rate differences between maximum and minimum temperature tolerance; thus, it is best to incorporate measurement error if seeking to compare clades suspected of occupying heterogeneous landscapes, and/or that do not occupy their full potential distributional areas.

Of course, several caveats apply to our results. We considered only the effects of realized niche truncation, yet ecological niche models may also extend niche estimates beyond true fundamental niche limits if extrapolation occurs beyond the conditions used in calibrating the model (Owens et al. 2013). Such extrapolation, unless the same amount occurs across all species, will cause rate estimates to increase, and will further complicate our understanding of niche evolution.

Our second caveat is that we imposed the same dispersal threshold across all species in a dispersal category to control for effects of niche truncation on evolutionary rates. Although we allowed dispersal to vary within this upper threshold, in real-world systems, dispersal ability may change more dramatically across species within a clade. A mixture of species with good and poor dispersal abilities will likely dampen the upward bias in the rate of BM evolution.

Third, the cellular automaton algorithm and dispersal thresholds that we implemented were intended to simulate realistic distributional patterns within the constraints of species' potential geographic distributions. These thresholds thus implicitly incorporated information on both dispersal and biotic constraints, both of which govern the geographic distribution of a species. Biotic and dispersal constraints, however, may not co-vary, producing a mixture of species with differing abilities to occupy their full potential distributions. Again, such a mixture is likely to dampen the upward bias in the rate of BM evolution.

Fourth, we focused on effects of niche truncation on rates of evolution. Incompletely-characterized traits may affect ability to detect phylogenetic signal in trait data. Using the same procedure as for σ^2, we assessed the degree to which niche truncation influenced estimates of phylogenetic signal by estimating both Pagel's λ (Pagel 1999, Freckleton et al. 2002) and Blomberg's *K* (Blomberg et al. 2003), as implemented in the 'phylosig' function in the R package 'phytools' v.0.5-38 (Revell 2012). In both cases, niche truncation resulted in significantly lower phylogenetic signal, particularly for minimum temperature tolerance (results not shown). When niche truncation was considerable (i.e., under poor dispersal thresholds), most species' realized niche simulations indicated no significant phylogenetic signal for minimum temperature tolerance. This missing evolutionary signal will again distort understanding of trait evolution, a situation exacerbated by the fact that environmental variables can show weak phylogenetic signal arising from empirical distributional data being collected at the wrong spatial scale or with geographic or environmental bias (Menke et al. 2009).

Finally, we did not consider effects of different evolutionary models on rate estimates. We simulated trait evolution using BM, and thus assessed rate estimates using this same model. When dealing with real-world data, however, it is important to select the best evolutionary model

based on the underlying data, which has been treated extensively elsewhere (Münkemüller et al. 2015). σ^2 estimation depends on the assumption of the underlying model of evolution, which should attempt to account for rate heterogeneity across a tree (Pennell et al. 2015). Assuming that niches evolve at one rate across entire clades is unrealistic and will result in erroneous evolutionary interpretations.

Regardless of these caveats, the analyses presented herein should serve as a caution for researchers attempting to analyze patterns of phylogenetic niche conservatism and niche evolution. Estimates of phylogenetic niche conservatism based on incompletely-characterized realized niches can lead to inflated rates of evolutionary change and result in inaccurate reconstructions of evolutionary patterns. Researchers should be aware of these potential biases and attempt to correct for them, potentially by including estimates of niche truncation in analyses.

Our results are not only relevant to studies of niche evolution, but to study of any traits that are prone to incomplete characterization. Such incomplete characterization could be caused by sampling variation; instrument-related error; variation by age, sex, season, or time of day; or low repeatability related to fluctuations in behavioral or physiological state (Ives et al. 2007). In these cases, rates of evolution may also be overestimated, and comparisons among clades should be made with caution and an eye for controlling for biases that may result in more truncation (i.e., more measurement error) in one clade over another.

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Figure Captions

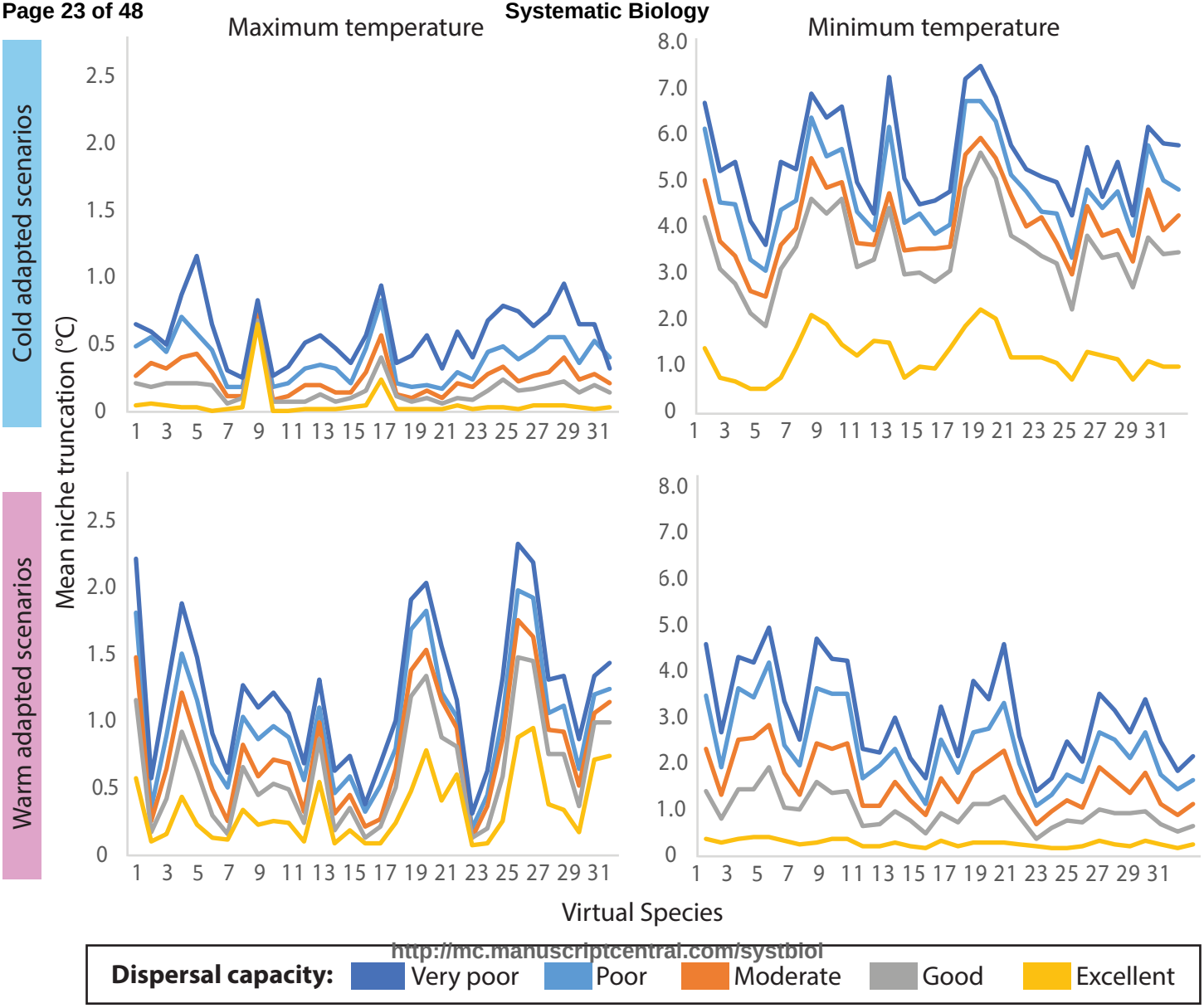
Fig 1. Mean per-species niche truncation (°C) across 100 replicates under each dispersal scenario for maximum (left column) and minimum (right column) temperature tolerances. For each species, niche truncation is averaged over 10 evolutionary scenarios characterizing the cold-adapted (top row) and warm-adapted (bottom row) clades. Note that data are presented as line graphs for ease of visualization, but each species on the x-axis is independent.

Fig 2. Rate of Brownian motion (BM) evolution (σ^2) for maximum (max) and minimum (min) temperature tolerance for each of 10 evolutionary scenarios for cold-adapted clades with very poor dispersal abilities (dispersal threshold = 12). The star represents the true rate of niche evolution based on simulated BM fundamental niche evolution, whereas the box plots show the estimated rates of niche evolution from 100 realized niche simulations (i.e., from realized niches). Both maximum and minimum temperatures were multiplied by 10 to convert to integers; rates reflect this multiplication.

Fig 3. Rate of Brownian motion (BM) evolution (σ^2) incorporating error rates for maximum (max) and minimum (min) temperature tolerance for each of 10 evolutionary scenarios for cold-adapted clades with very poor dispersal abilities (dispersal threshold = 12). The star represents the true rate of niche evolution based on simulated BM fundamental niche evolution, whereas the box plots show the rates of niche evolution approximated from 100 realized niche simulations. Both maximum and minimum temperatures were multiplied by 10 to convert to integers; rates reflect this multiplication.

Fig 4. Variance in minimum and maximum temperature values associated with species' potential suitable areas for both cold- and warm-adapted clades. Temperature values are centered and standardized to compare maximum and minimum values on the same scale. Results were averaged across species and evolutionary scenarios, given that individual per-species and per-scenario variances were similar.

Fig 5. Per-species variance in maximum and minimum temperature values across the 100 distributional replicates. The 32 virtual species are represented on the x-axis for both warm-adapted and cold-adapted clades. The blue line denotes minimum temperature tolerances, whereas the red line represents maximum temperature tolerances. Patterns were similar across dispersal scenarios, so we provide averages here. Data are presented as line graphs for ease of visualization, but each species on the x-axis is independent. ES = evolutionary scenario.



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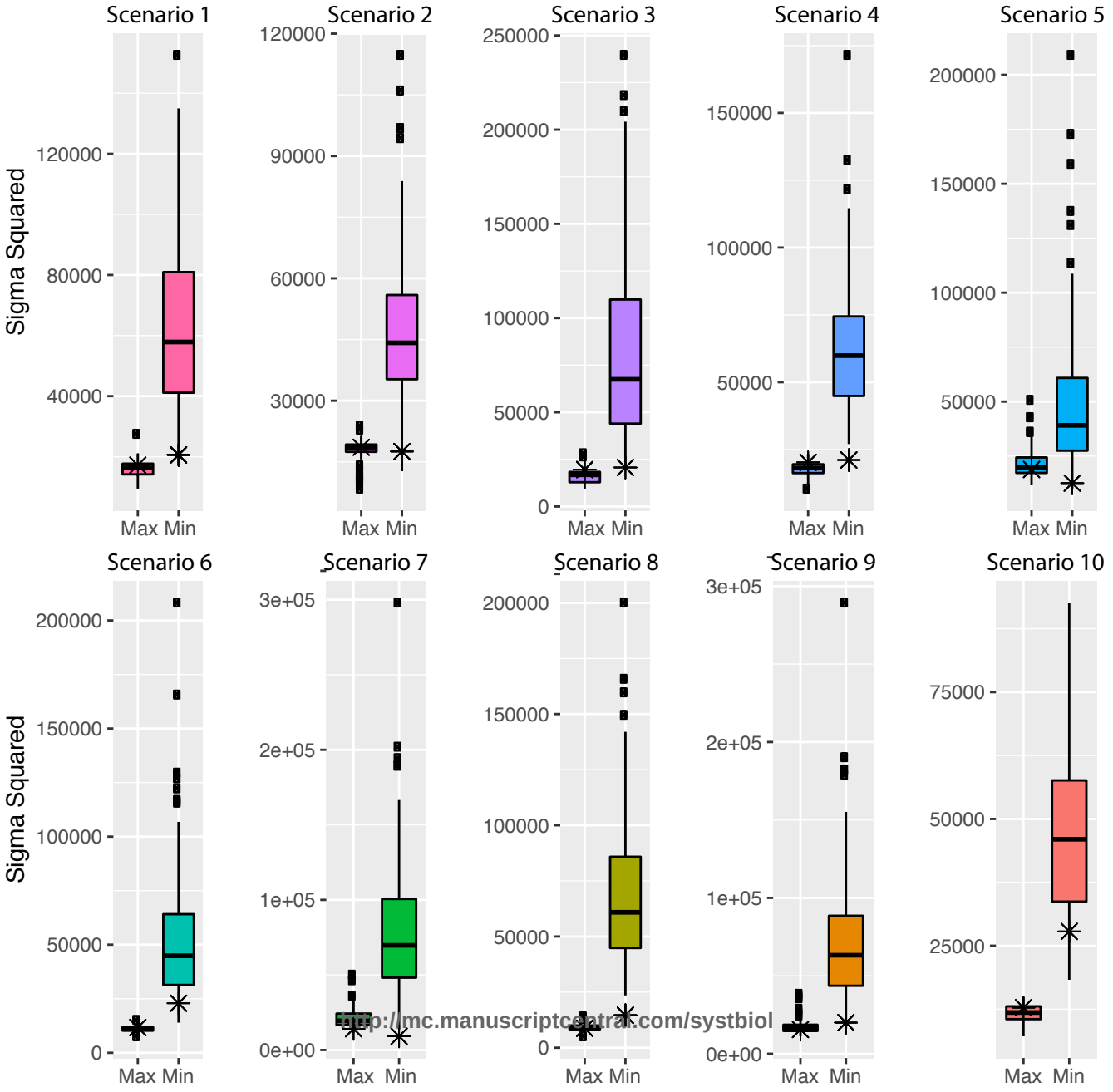

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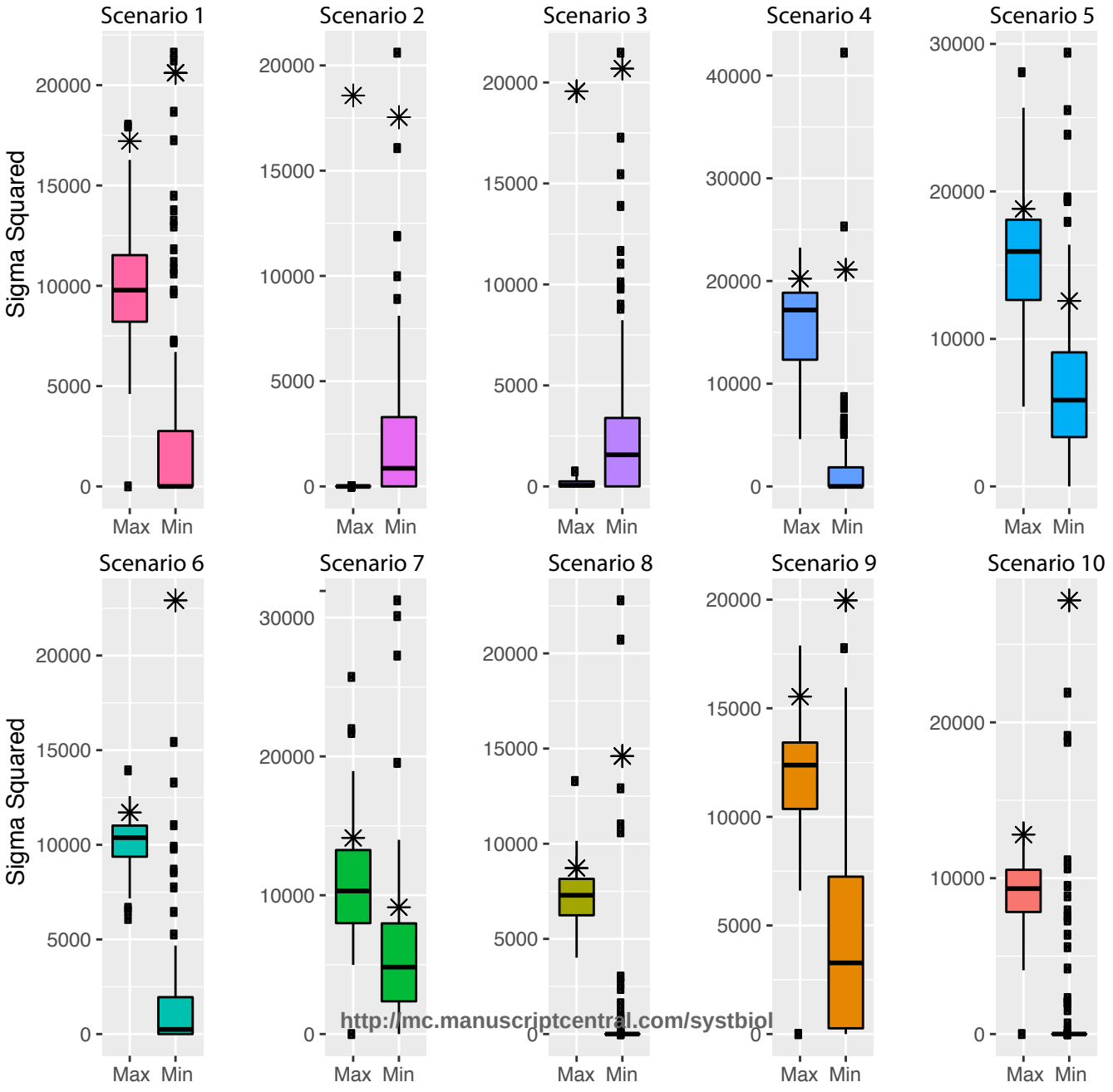
Cold-adapted, poor dispersal scenarios — error estimated



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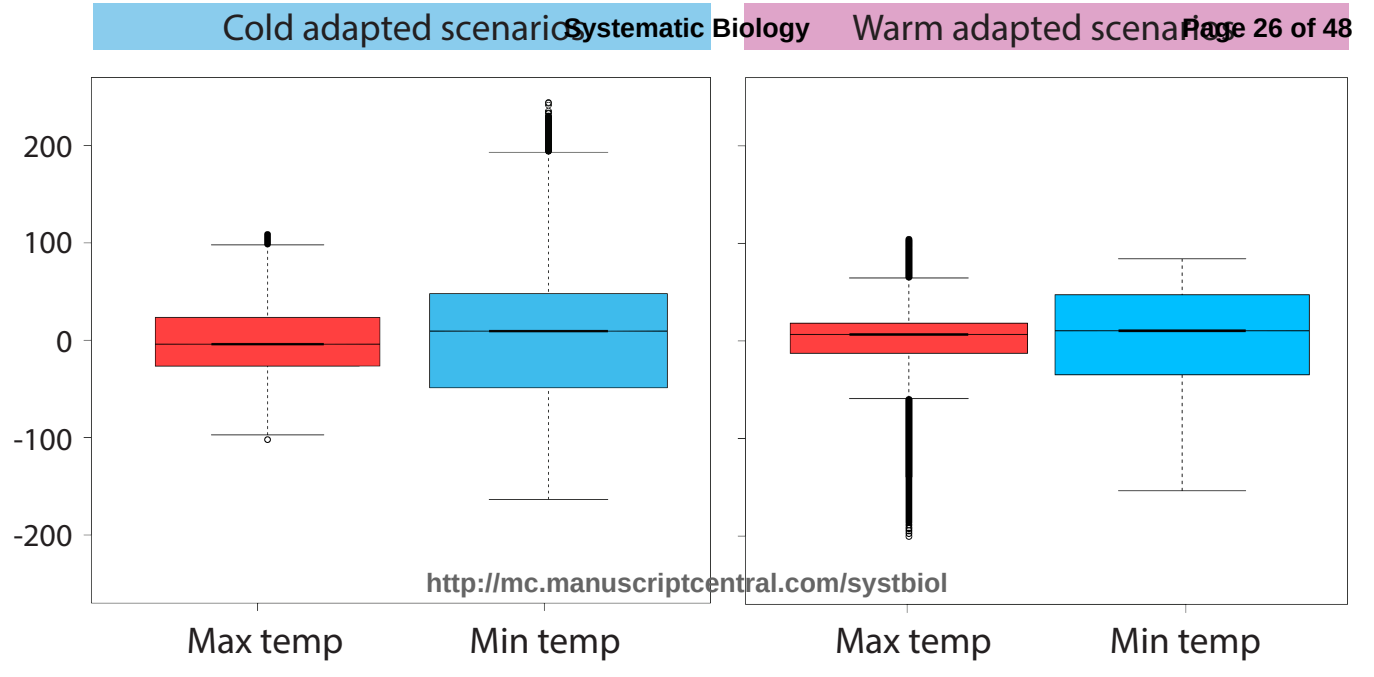

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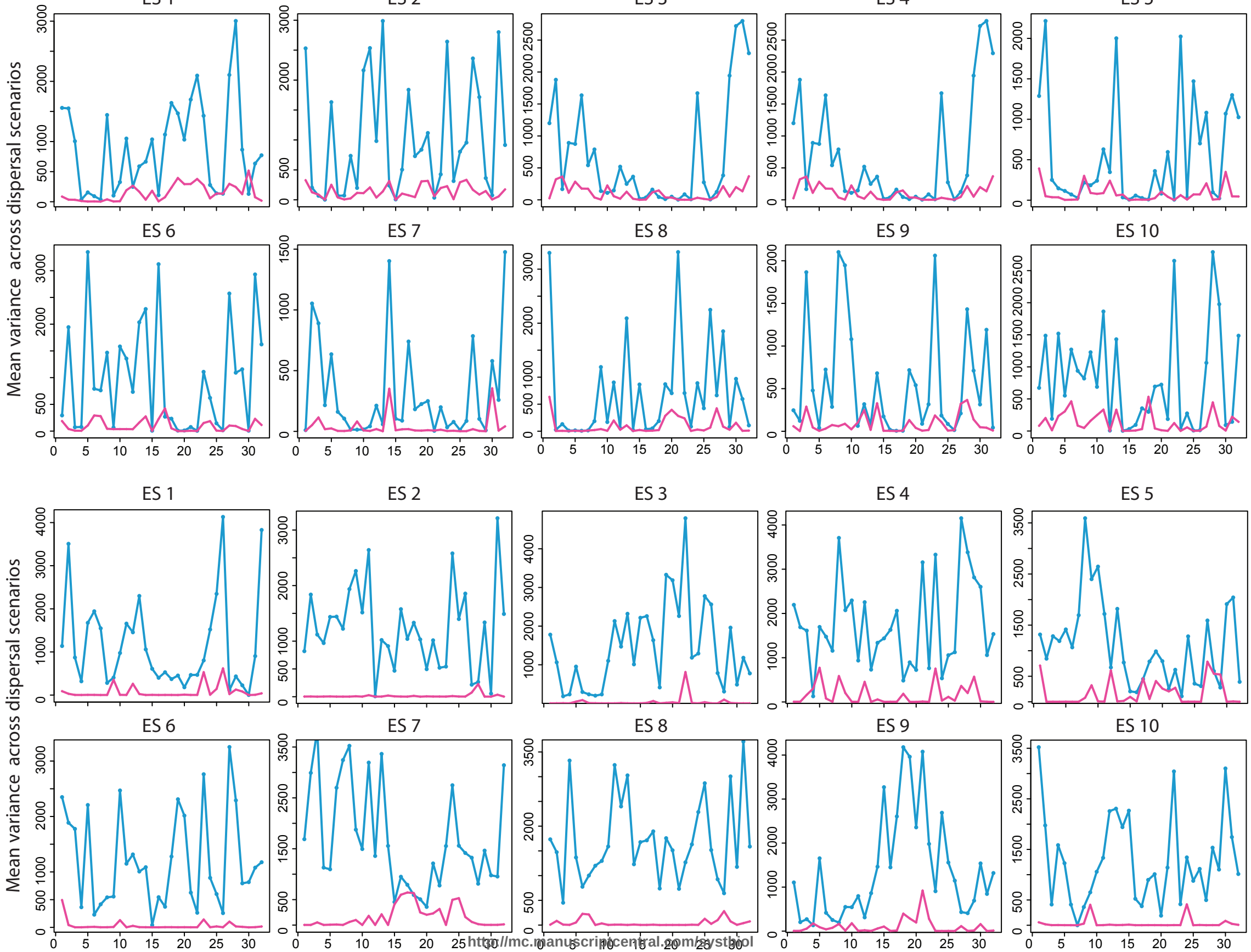
Warm-adapted scenarios

Cold-adapted scenarios



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