

Temporal variability of carabid beetles as a function of geography, environment,  
and species

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## Abstract

Populations of species fluctuate through time and across geographic space. Identifying the potential drivers of temporal variability in population dynamics is a fundamental aim of population ecology, with clear implications to understanding population extinction risk, the influence of diversity on composite community scale variability, and the extent to which temporal variability is driven by exogenous (e.g., climate) or endogenous (e.g., life history) factors. We used data from the National Ecological Observatory Network (NEON) consisting of over 750 carabid beetle species systematically sampled between 2013 and 2021 across 47 terrestrial sites in the United States of America to examine the relative roles of geographic location, environmental gradients, and species identity on temporal variability. We find an effect of species taxonomic identity on resulting temporal variability in abundance both at site-level and taxonomy-level scales. Environmental variables (mean annual temperature and precipitation and seasonality in temperature and precipitation) and geographic position (latitude and longitude) were not strongly related to temporal variability, and there was no spatial signal in site-level mean temporal variability. The importance of species to temporal variability highlights the role of life history differences across species, resulting in a mean shift in population growth rate, as a potentially more important driver than aspects of site and environment that may relate more to temporal changes in population growth rates.

# Introduction

Population dynamics are the result of multiple interacting processes which may influence species demographic rates (Oro, 2013; Ovaskainen and Cornell, 2006). Quantifying and understanding fluctuating populations is important, as these fluctuations may be a precursor to population extinction (Ovaskainen and Meerson, 2010), may be related to community level properties (Dallas and Kramer, 2022), or may highlight the role of biotic interactions on population dynamics (Brännström and Sumpter, 2005; Breton and Addicott, 1992; Hudson et al., 1992). Therefore, understanding how and why populations vary through time is a fundamental goal with clear implications to conservation and management efforts. Further, determining the drivers of fluctuating populations is a central goal in population ecology, with a large body of empirical and theoretical work aimed at disentangling the roles of species life history, demographic stochasticity, and environmental drivers leading to temporal variability in population dynamics (Bjørnstad and Grenfell, 2001; Boyce et al., 2006; Lundberg et al., 2000; Tuljapurkar, 1982). Understanding population variability is even more pressing in the face of climate change, as estimates of species temporal variability have been increasing in more recent years (Inchausti and Halley, 2002) and may provide insight into resilience following a disturbance (Hakspiel-Segura et al., 2022). Here, we define temporal variability as the variation observed in time series data of species abundances at a given location, and acknowledge the influence of spatial and temporal scale in the estimation of temporal variability (Clark et al., 2021).

Previous studies of temporal variability have largely considered two different forces. First, temporal variability may be a function of the environment (Bjørnstad and Grenfell, 2001). This would occur through environmental constraints on species demographic rates (e.g., temperature influencing birth or death rates) or through the effect of environmental variability on population dynamics (i.e., more variable environments may result in more variable population dynamics; (Chisholm et al., 2014)). Second, species intrinsically vary in their demographic rates and generation times, suggesting that temporal variability may be a function of species

identity or life history (Majeková et al., 2014). Apart from these exogenous (environment) and endogenous (species demography) forces, it is also possible that temporal variability is influenced by the biotic context of interacting species or some unmeasured aspect of the site (e.g., resource availability). That is, interacting species (e.g., competitors, mutualists, natural enemies) may strongly influence species abundances, resulting in changes to temporal variability. However, there is no clear consensus on how this would manifest, as species interactions could potentially decrease (Tilman et al., 1998) or increase (Arnoldi et al., 2019) temporal variability in some focal species. This creates a situation where temporal variability may be driven by environmental conditions, species identity, or site-level effects.

We explore the relative roles of geographic location, environmental variability, and species identity on temporal variability in population dynamics of over 750 carabid beetle species sampled across 47 terrestrial sites in the United States of America as part of the National Ecological Observatory Network (NEON). Carabid beetles are a speciose group of invertebrates commonly used as indicator species for arthropod diversity (Pizzolotto et al., 2018; Rainio and Niemelä, 2003), land use change (Niemelä, 2001), and restoration effort success (Sprössig et al., 2022). Short generation times, sensitivity to environmental change, and easily replicated sampling make this group ideal for exploring patterns of temporal variability in population dynamics across spatial and environmental gradients (Lövei and Sunderland, 1996; Marrec et al., 2017; Niemelä, 2001). We explored all combinations of geographic location, environmental variability, and species identity in models of temporal variability for each beetle species at each site. Aggregating estimates of temporal variability as a function of both site and species, we also explored the existence of spatial and phylogenetic signals in mean temporal variability. This attempts to condense estimates of temporal variability to either be a species or a site-level trait, allowing us to identify specific beetle species or specific geographic locations with particularly high (or low) temporal variability.

## Methods

**NEON ground beetle data** The National Earth Observatory Network is a National Science Foundation funded effort to monitor biodiversity, ecosystem processes, and abiotic variables across a total of 47 terrestrial sites in the United States (Kao et al., 2012) (see Figure 1a for the spatial distribution of sampling sites). The ground beetle data specifically offer an ideal system to explore temporal variability as a function of geography and species identity, as the beetles are typically sampled every two weeks, with the data included here being sampled between 2013 and 2021. Ground beetles are a species-rich group with a total of 762 unique species sampled as part of this effort. Beetles were sampled using pitfall traps, with a total of 10 plots per each sampled site. Each plot was composed of 4 pitfall traps, roughly 20m from the center of the plot, making a total of 40 traps per site. Traps were deployed for 10 consecutive days when temperatures were greater than 4 °C, meaning that the number of sampling periods per site varied non-randomly with climatic conditions, in which colder sites were not sampled as much of the year, as beetles would not be active during these cold periods.

We estimated species abundance as the total number of beetles of a given species sampled at the site level, standardized by the number of trap nights (number of days times number of traps for that sampling period). It is important to note the assumptions that this approach of abundance estimation may implicitly make. For instance, abundance is estimated at site level, which ignores trap-level variation in beetle counts. Further, abundance estimates are based on the number of beetles in each trap, which assumes that beetles encounter a trap with equal probability across time, though it is possible that dips in abundance are not a result of changes to abundance, but simply of climatic drivers resulting in reduced beetle mobility. These are all issues not restricted to this particular data resource, but nearly omnipresent issues in the types of ecological data we often collect (Martin et al., 2011). Methods developed around distance-based sampling and Bayesian models attempting to estimate uncertainty in population sizes are one clear step forward, though a hierarchal model fit across traps, sites, species, and sampling times would

likely become unwieldy.

**Climatic data** Species temporal variability may be driven by the environmental conditions. We considered temperature and precipitation as potential drivers of population variability, specifically considering the mean and variability in monthly estimates of temperature and precipitation, with data extracted from the PRISM data (PRISM Climate Group, 2023), using the `prism` R package (Hart and Bell, 2015). Specifically, for each species and site combination, we extracted monthly values of temperature (minimum, mean, and maximum) and precipitation for the period encompassing the first and last sampling months where a given species was found in a given site. This allows us to relate the mean and variability in climate to each species when the species was sampled at a given site, in an attempt to make estimates of temporal variability comparable to the mean and variability in climate during that period. The biological interpretation of the importance of mean climatic conditions compared to the variability in climatic conditions is substantial. We analyze both, with the influence of mean conditions in the Supplemental Materials, and a focus here on climatic variability, as the influence of fluctuating environments on population dynamics is a long-standing and important question (Kremer et al., 2018; Ovaskainen and Cornell, 2006; Tuljapurkar, 1982, 1989).

**Expectations from theory** Mean temperature may drive temporal variability if warmer (or cooler) conditions consistently change population growth rates. The underlying idea is that if population growth rate scales with mean temperature or precipitation, we expect that temporal variability would be higher for populations with lower population growth rates (see Supplemental Materials for a demonstration with the Ricker model). To explore mean conditions, we calculated the mean of the monthly climate estimates for each species-site combination (see Supplemental Materials). We focus here on how temporal variability in climatic conditions could influence temporal variability in population dynamics. To do this, we quantified environmental variability using the  $D$  statistic (described below in Equation 1) on monthly estimates of temperature and precipitation for each

species-site combination. We might expect climatic variability to have a positive relationship to population temporal variability, as more variable environments may yield more variable population dynamics. Further, we explored how temporal variability in demographic parameters – a form of environmental stochasticity – could influence resulting temporal variability in population dynamics (see Supplemental Materials). Finally, we explored how differences in species mean growth rates and temporal variability in growth rate interacted to produce expectations from the Ricker model. This provides a context for the importance of species relative to the importance of environmental variability, as shifts in mean population growth rate independent of time would reflect differences among species, while temporal variation in growth rates is more representative of environmentally-driven temporal variability in population dynamics (see Supplemental Materials). Together, we find that temporal variability in population dynamics is reduced by large population growth rates (Figure S1), low temporal variability in population growth rates (Figures S2-S4), and not strongly influenced by temporal variation in intraspecific competition (Figure S2). Together this highlights how shifts in mean population growth rates (perhaps capturing species-level life history differences) and temporal variation in growth rates (perhaps capturing environmental variability) interact to produce variability in population dynamics.

**Calculating temporal variability** To estimate temporal variability in time series of population and community abundance, we used the consecutive disparity index ( $D$ ; (Fernández-Martínez et al., 2018)). This measure has been previously used to estimate interannual climatic variability (Meseguer-Ruiz et al., 2017) and fruit production (Vergotti et al., 2019), and is measured as

$$D = \frac{1}{n-1} \sum_{t=1}^{n-1} \left| \ln \left( \frac{p_{t+1} + k}{p_t + k} \right) \right| \quad (1)$$

where  $p_t$  corresponds to abundance at time  $t$ , where the entire length of the time series is  $n$ , and  $k$  is a constant. This value  $k$  is used to ensure that zeroes do not strongly influence the  $D$  statistic. To make estimates of  $D$  comparable across



different time series, we considered  $k$  to be 1% of the time series mean, as suggested by the creators of the measure (Fernández-Martínez et al., 2018). The  $D$  statistic takes the temporal structure of the time series into account, in that the order of the values influences the resulting measure of variability. This is a benefit of the approach, as measures of variability which do not consider population dynamics may fail to capture large changes in population dynamics across short-timescales. However, the data we use here are limited in that they can be sampled at irregular intervals, creating time series in which values may have long temporal gaps. To explore how this influences our estimates of temporal variability, we also estimate temporal variability using the coefficient of variation, as this measure does not take the temporal order of the values into account. We found qualitatively similar results when estimating temporal variability as the coefficient of variation ( $CV$ ) instead of the  $D$  statistic (see Supplemental Materials).

**Partitioning site, environmental, and species effects on temporal variability** We fit linear models which included individual and combined effects of site-level covariates and species identity, as a way to explore shared variance explained and the independent contributions of geographic space and species. All models included the effect of the average number of sampling events per species at each site, a variable which in isolation from any other variable resulted in an adjusted  $R^2$  of 0.002. We expanded this baseline model to include a suite of different models with increasing complexity. First, we incorporated the effects of site by including the mean latitude and longitude at a given site (and the interaction between these two variables). This was done in place of using the site name, as we would expect nearby sites to have more similar dynamics, and wished to capture the influence of continuous space. It is possible that incorporating space in this manner misses some key context, such as two sites separated by a mountain range or other dispersal barrier.

Next, we considered the influence of species by treating species identity as a factor. Note that this requires the fitting of over 500 coefficients and will not consider the actual taxonomic relationships among species at higher taxonomic levels.

However, this model will consider each species to respond uniquely in terms of temporal variability. That is, independent of climate and site, is species name related to corresponding temporal variability? Finally, we considered the effects of environment by including either the mean or the variability in temperature and precipitation for each site-species combination. These were treated separately due to the collinearity between them (there was clear negative mean-variance scaling for minimum, mean, and maximum temperature as well as precipitation; see Supplemental Materials), and the different paths through which they may operate. That is, mean environmental conditions may influence demographic rates independent of variability, but variability around a suitable mean environment could lead to more variable population dynamics. Models including environmental variability nearly always had higher performance. We report on the influence of environmental variability here, and explore the role of mean environmental conditions in the Supplemental Materials.

We considered every combination of the three variable groups – site (latitude, longitude, and their interaction), environment (variability in minimum, mean, and maximum temperature, and precipitation), and species (taxonomic name) – for a total of 7 models. Every model also contained the average number of sampling events per species at each site. Model performance was estimated as adjusted  $R^2$ .

**Species and geographic signals in mean temporal variability** After partitioning the effects of geography and species on resulting temporal variability, we explored the potential for there to be a signature of site or species on aggregate properties. That is, are there signatures in mean species-level temporal variability across sites, or mean site-level temporal variability for a given community, which could signal the importance of species or site constraints on average temporal variability. We explore the potential existence of spatial autocorrelation in site-level temporal variability by computing Moran’s  $I$  statistic on the mean temporal variability at each site. Distance between all sites was estimated as Haversine distance using the `geosphere` R package (Hijmans, 2021).

We explored species-scale signals in mean temporal variability by considering beetle taxonomic relationships for the set of 762 carabid beetle species in the NEON data. We constructed the phylogeny based on the taxonomic data obtained from NCBI through the `taxize` R package (Chamberlain and Szocs, 2013). To obtain mean temporal variability estimates at the species level, we calculated the weighted mean  $D$  statistic, weighted by the number of times the population was sampled at each site (Figure 1). That is, we are more confident in estimates of temporal variability based on sites that have been more thoroughly sampled. We tested for a phylogenetic signal in mean temporal variability across the beetle species phylogeny using both Pagel’s  $\lambda$  and  $K$  statistics, computed using the `phytools` R package (Revell, 2012).

*R* code and data to reproduce the analyses is provided at <https://doi.org/10.6084/m9.figshare.21217709>

## Results

**Partitioning site, environmental, and species effects on temporal variability** The baseline model, including only the average number of sampling events per species, had an adjusted  $R^2$  of 0.002. The average number of sampling events per year was positively related to temporal variability ( $\beta = 0.003$ ,  $p = 0.03$ ), potentially highlighting spatial variation in average temporal variability, either as a function of species responses to variable environments, or because sites in colder climates (higher latitudes) tended to have more limited sampling. Building on this baseline model, we considered the roles of species identity, site, and environmental variability on species temporal variability. The full model containing site level (latitude and longitude and an interaction term), environmental (temporal variability in temperature and precipitation), and species level (species identity) covariates had an adjusted  $R^2$  of 0.246. We found that environmental (adjusted  $R^2 = 0.012$ ) and site (adjusted  $R^2 = 0.004$ ) submodels performed poorly, especially considering the relative importance of the species identity submodel (adjusted  $R^2$

= 0.165). Finally, we would expect that more variable environments would correspond to more variable population dynamics (Tuljapurkar, 2013). We find that in models incorporating environmental variability, precipitation variability is the only variable to have an effect ( $\beta = 0.12$ ;  $p = 0.03$ ), but no environmental variability predictors were significant in any other composite model. Together, this suggests that species identity – or the combination of species identity and environmental variability – were the most important predictors of temporal variability in population dynamics (Figure 2). These findings were very similar when considering mean environmental conditions instead of environmental variability (see Supplemental Materials).

**Species and geographic signals in mean temporal variability** The geographic model described above did not explain an appreciable amount of variation in temporal variability. This was seconded by our lack of ability to detect spatial autocorrelation in mean temporal variability at each site, as we observed significant *negative* spatial autocorrelation in site-level mean temporal variability (observed = -0.056, expected = -0.02,  $p = 0.007$ ), suggesting that temporal variability estimates across space were actually more variable across space than expected. The importance of species identity to temporal variability estimates could be a function of the distribution of species, as widespread species may have more estimates of temporal variability (discussed further in the Supplement). Future work exploring temporal variability for a single species across its geographic range will help clarify how species fluctuate across their range.

Apart from geographic range size, other factors may lead to some species fluctuating more than others. To explore the existence of a phylogenetic signal in mean temporal variability at the species level, we computed the weighted mean temporal variability for each of the 762 species in the data, where estimates of temporal variability were weighted by the number of times the site was sampled (Figure 3). Both approaches found a significant phylogenetic signal in weighted mean temporal variability ( $\lambda = 0.177$ ,  $p = 0.0009$ ;  $K = 0.256$ ,  $p = 0.037$ ). These results were the same when we estimated temporal variability using the coefficient of variation

instead of the  $D$  statistic (see Supplemental Materials). However, the species with highest temporal variability were not the same set when using  $CV$  instead of  $D$ , despite the two measures being strongly correlated (Pearson's correlation = 0.67,  $p < 0.0001$ ).

## Discussion

Understanding the drivers of population dynamics is a fundamental aspect of population ecology. Specifically, the relative importance of environmental drivers and intrinsic demographic characteristics of species is key to our understanding of the spatial distribution of population variability. We explored temporal variability in beetle population dynamics distributed over much of the United States of America, finding that environmental variability and species identity were associated with temporal variability in beetle population dynamics. This highlights the role of species differences in demographic rates, generation times, and other relevant life history variables, in concert with environmental variability, on resulting temporal variability in population dynamics. This importance of environmental variability and species identity was further supported through simulating species dynamics following a Ricker model, modifying population growth rate means and temporal structure (see Supplemental Materials). When aggregating temporal variability estimates to the site and species scale, we find negative spatial autocorrelation in mean temporal variability, and a clear phylogenetic signal in species mean temporal variability, further strengthening our findings that species identity is important to temporal variability, and that temporal variability is conserved across the carabid beetle taxonomy. Taken together, we provide evidence for the importance of species identity on temporal variability in population dynamics for a large set of carabid beetle species, highlighting the role of conserved demographic rate variation relative to the influence of the environment.

Species identity was more important than site or environmental variability to carabid beetle temporal variability. The importance of species was further highlighted by a clear phylogenetic signal in mean temporal variability for the set of

carabid beetle species. Species differ in their demographic rates (Pironon et al., 2017), and this species-level demographic trait variation may override the effect of environmental variables on demographic rates themselves (Pironon et al., 2018). It is important to note that the environment could still exert strong pressures on demographic rates, but species may buffer the potential resulting effects on population dynamics through mechanisms such as demographic compensation (Forcada et al., 2008) or changes which are undetectable without more detailed sampling, such as changes in life history, body size distribution, or behavior (Ergon et al., 2001). For instance, species in more variable environments can exhibit adaptive demographic lability, in which birth or death processes track environmental fluctuations in a manner to temper the negative effects of temporal variation in environmental conditions (Koons et al., 2009; Le Coeur et al., 2022). At a coarse scale, this could be explored using the mark-recapture data as part of some NEON data collection, but without corresponding individual level demographic information (e.g., reproductive output for a given individual per year), it is difficult to address the role of demographic lability in buffering NEON populations from the effects of environmental variability. Future theoretical development linking demographic and environmental stochasticity to temporal variability (see Supplemental Material) by considering the spatial and temporal distributions of species demographic parameters is needed to further disentangle how temporal variability is influenced by site, species, and climatic variability.

The lack of contributed information from geographic and environmental variables in our models is counter to ideas around drivers of fluctuating populations (Kareiva, 1990; Krebs, 2013; Pironon et al., 2017). For instance, populations at the edge of a species geographic range are hypothesized to be smaller and more variable as a function of either limited dispersal or harsher environmental conditions at the species range margin (though this conflates geographic and environmental space somewhat). While the NEON data provide systematic community level sampling of beetles, the distribution of sites is limited, and almost certainly not representative of a species entire geographic range. We can see this in the number of sites

where species were sampled, with many species sampled in only a few sites (see Supplemental Figure S8). As such, more finely resolved spatial sampling would be necessary to address questions of temporal variability across a species range.

The importance of species identity, and the subsequent conservation of temporal variability across species ranges, was also observed when aggregated to the species level. That is, when we considered the mean temporal variability per species, we observed a clear phylogenetic signal in temporal variability, further suggesting that evolutionary history and life history variation were underlying temporal variability for carabid beetles. It is possible that carabid beetles might be unique in the degree of life history and functional trait variation present (Fountain-Jones et al., 2015), suggesting that the importance of species to temporal variability may be weaker for other taxonomic groups. The repeated and systematic sampling of multiple taxonomic groups as part of the NEON data collection effort provides data to test the importance of taxonomic group on resulting patterns of temporal variability. For instance, dispersal dynamics were unlikely to influence temporal variability in beetles, as sites were generally >100km away from one another or more, but this could be an important force for some taxa (Wang et al., 2015) or at smaller sampling scales (Den Boer, 1970). Finally, it is important to consider the inherent burstiness of populations and how this affects estimates of temporal variability. That is, beetle dynamics were strongly seasonal, with a clear annual cycle. Detrending the data would ablate important aspects of population dynamics. We observed a positive relationship between mean temporal variability estimated per year and the overall temporal variability, suggesting that no one aberrant year was responsible for driving temporal variability across the time series. We further explore this, as well as different estimates of temporal variability (coefficient of variation instead of the  $D$  statistic) in the Supplemental Material. The importance of species should be considered in future theoretical models through the incorporation of variation in species demographic parameters and shared responses to environmental variation as the potential underlying mechanism for the importance of species we observed. Estimates of beetle life history variation and

species response curves to environmental drivers would further strengthen the link between theoretical findings and observational data in natural systems.

Species fluctuations in population dynamics may be driven by seasonal fluctuations in environmental conditions (as noted above). Yet, if these responses to environmental conditions are consistent across the species geographic range, it is possible that environmental variables are unrelated to population fluctuations. This creates an interesting possibility, in that species life history variation is more important for temporal variability in population dynamics than the environment. Regardless of this point – which certainly warrants further exploration – we found that carabid beetle species identity was the most important predictor of temporal variability, and that mean temporal variability for species was related to beetle taxonomic relationships. Temporal variability has previously been used as an estimate of stability, highlighting the importance of species differences in potential stability relative to the influence of environmental variables. That is, relationships relating species diversity to mean temporal variability (McCann, 2000) could benefit from exploring *which* species appear in species-rich communities, as non-random species turnover and competition may select for more stable species independent of any influence of species interactions on resulting community-level *stability*. Finally, theoretical development linking species identity, changing environments, and dispersal connections with nearby habitats will start to disentangle the relative roles of demographic stochasticity, demographic heterogeneity, environmental stochasticity, and dispersal (Melbourne and Hastings, 2008). Fitting stochastic models to longer-term time series data is one way to link observations in experimental systems to these driving forces (Dallas et al., 2021; Melbourne and Hastings, 2008), and this is an important and challenging next step for understanding fluctuating population dynamics in natural populations.



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## Figures

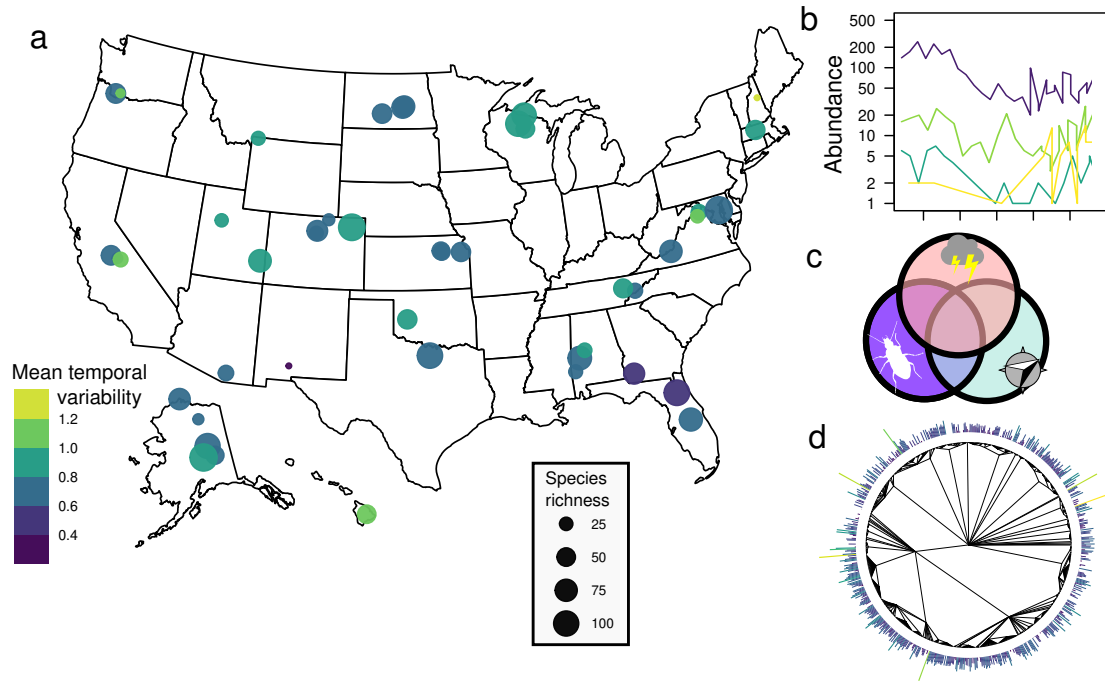


Figure 1: The spatial distribution of carabid beetle sampling sites across the United States (panel *a*), where point size is proportional to the overall species richness in the site, and color is proportional to the mean temporal variability estimate. Using these time series data on species abundances (panel *b*), we estimated the relative importance of geography, environmental variability, and species identity on resulting temporal variability (panel *c*), and explore species-level phylogenetic patterns in mean temporal variability values (panel *d*).

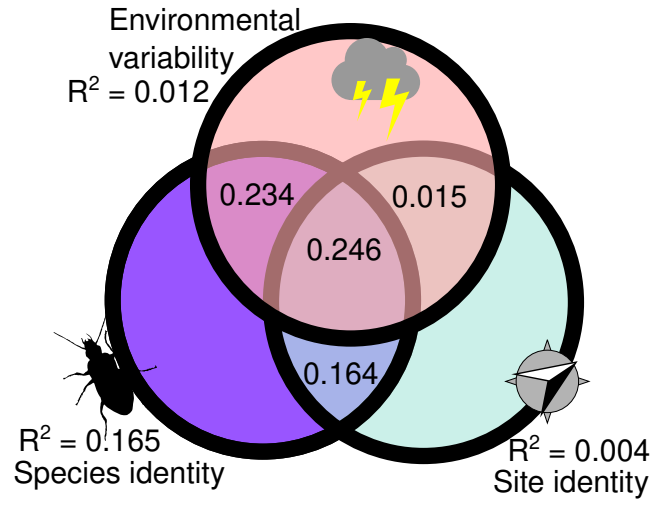


Figure 2: Adjusted  $R^2$  values for each submodel containing different combinations of geographic location (latitude and longitude of site; lower right component), environment (variability in monthly temperature and precipitation; top component), and species identity (lower left component) on temporal variability. For instance, the model containing geographic location and environment is the overlapping region in the top and right circles, and this model had an adjusted  $R^2$  value of 0.015.

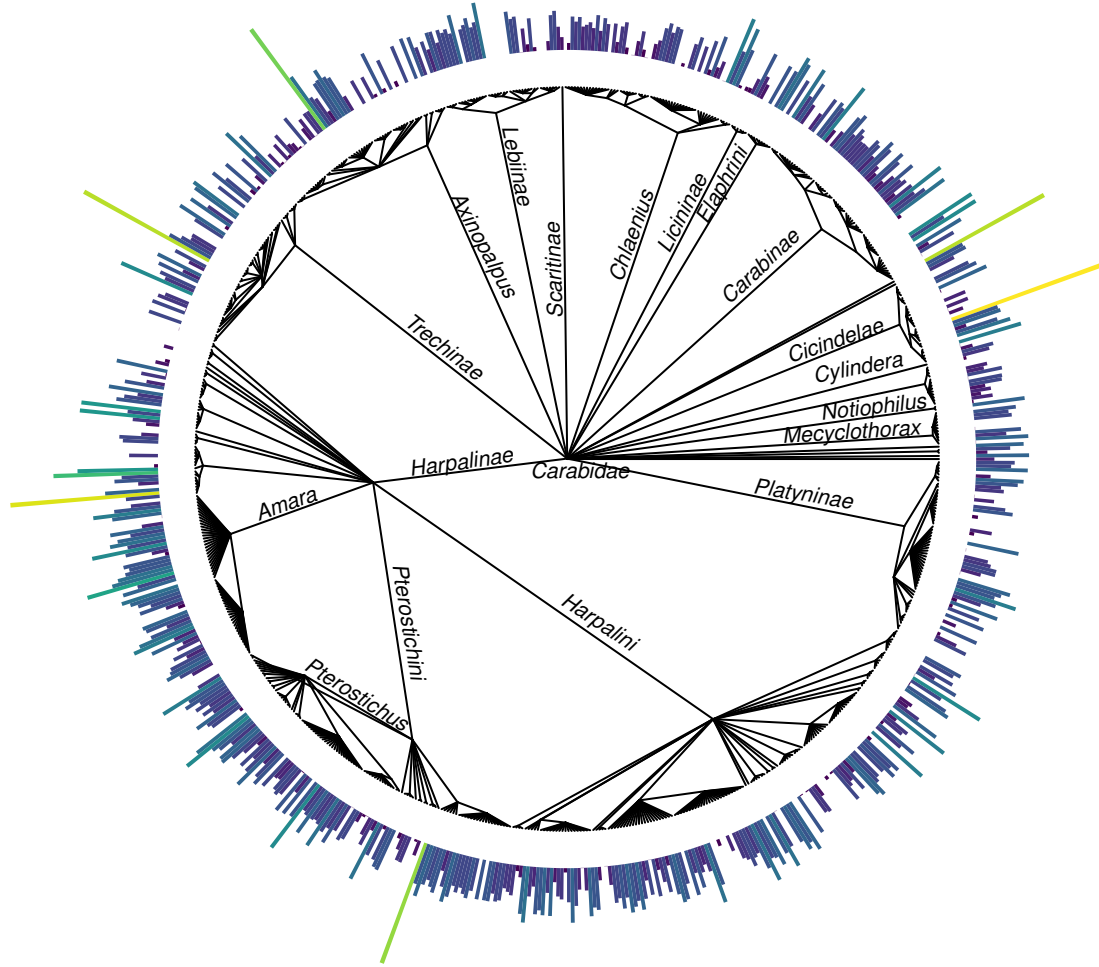


Figure 3: The distribution of mean temporal variability ( $D$  statistic weighted by the number of sampling events per site) across the ground beetle phylogeny (height and color of bars corresponds to mean temporal variability for a given species). Species with especially high temporal variability included *Cicindela abdominalis*, *Bembidion ampliatus*, and *Calosoma wilcoxi*.



# Appendix A

Temporal variability of carabid beetles as a function of geography, environment, and species

Tad A Dallas, Cleber Ten Caten, and Lauren A Holian

## Temporal variability is related to population growth rate

Temporal variability, estimated using either the  $D$  statistic or the coefficient of variation, should depend on population growth rate. Populations which quickly approach carrying capacity and achieve quasi-equilibrium quickly should have lower temporal variability. Even in stochastic models, where equilibrium may not be reached, we might expect that larger population growth rate values would lead to more stable population dynamics. This, of course, is only true for a reasonable set of population growth rates, as the logistic map identifies a large set of population growth rate space in which temporal variability would be rather high (e.g., during period doubling cycles and chaos). For completeness, we simulate population dynamics from a stochastic Ricker model here to demonstrate the scaling between temporal variability and population growth rate.

The Ricker model was structured as a discrete time model where population in the next timestep ( $N_{t+1}$ ) was a function of the current population size at time  $t$  ( $N_t$ ) and the population growth rate ( $R$ ), modified by the effects of density-dependent competition ( $e^{-\alpha N_t}$ ).

$$N_{t+1} = N_t R e^{-\alpha N_t} \quad (2)$$

Stochasticity was introduced into this simple model by treating the number of offspring per individual to be a Poisson random variable and treating survival as a binomial random variable. We simulated this model, holding  $\alpha$  constant at 0.01 and allowing population size to vary ( $N_t = [10 - 500]$ ). Across a gradient of 100 population growth rates ( $R = [0.9 - 2.25]$ ), we simulated population dynamics 100 times for each growth rate. We calculated the  $D$  statistic as an estimate of

temporal variability, considering only those populations which did not go extinct by the end of the 1000 timesteps. We found a clear negative relationship between temporal variability and population growth rate, suggesting that large population growth rates tended to have less variable population dynamics (Figure S1).

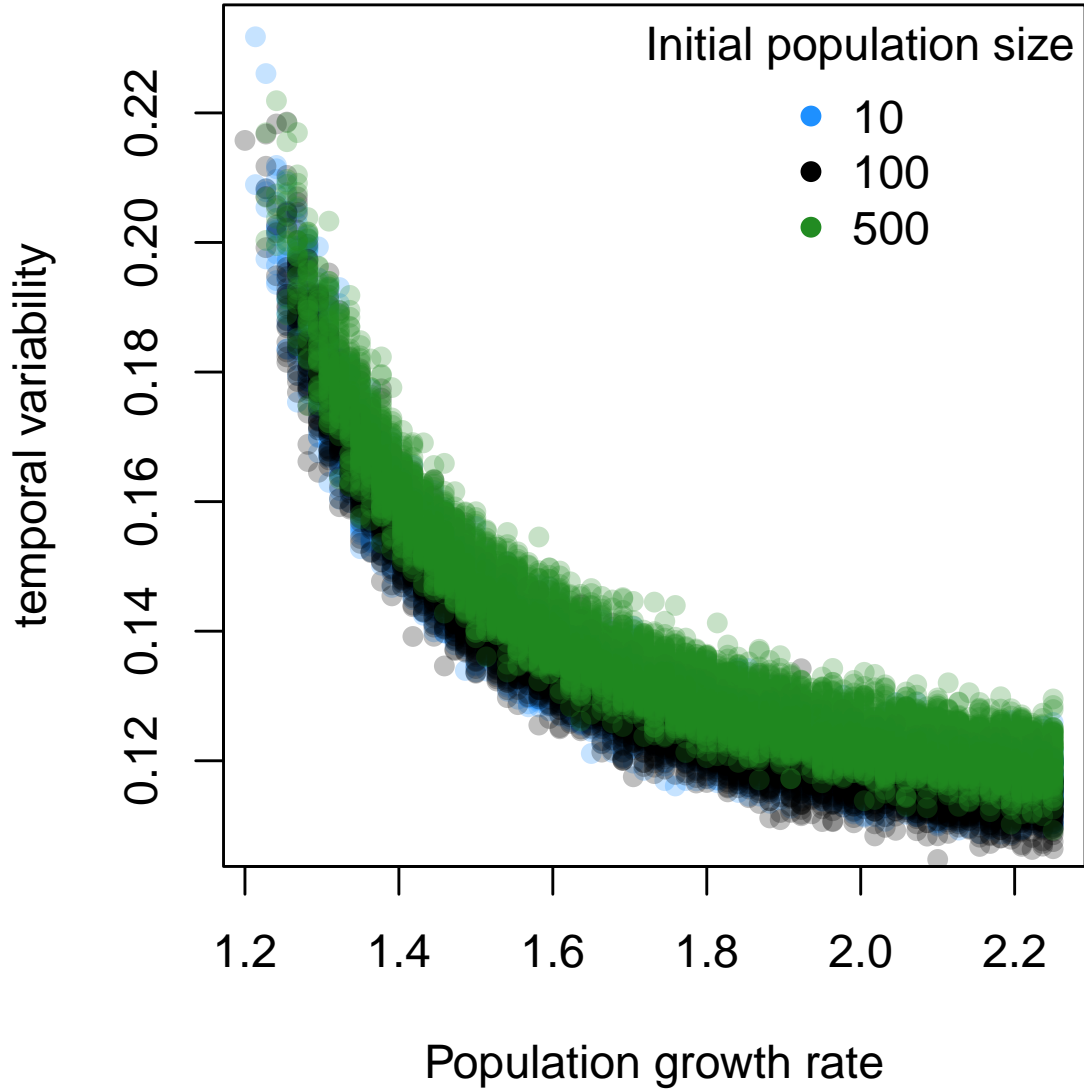


Figure S1: Temporal variability – quantified using the  $D$  statistic – was negatively related to population growth rate for a large set of simulated population dynamics following the Ricker model ( $\alpha = 0.01$ ). This scaling was not influenced by initial population size.

## More variable environments lead to more variability in population dynamics

We can extend the above Ricker model to incorporate environmental stochasticity, which we consider as temporal variation in population growth rate ( $R$ ) and competition ( $\alpha$ ) through time. We implement this as white noise, sampling values of  $R_t$  and  $\alpha_t$  from a normal distribution with some variance  $\sigma$ . By modifying  $\sigma$ , we modify the degree of spread in the temporal distribution of our demographic parameters. We consider a range of 100 values of  $\sigma$  for each demographic parameter  $R$  (0-0.5) and  $\alpha$  (0-0.01), looking at every combination of the two parameters (10000 combinations total). This variance parameter was on top of a mean growth rate  $R$  of 1.5 and mean  $\alpha$  of 0.03. Values of  $\alpha$  below 0 do not make sense biologically, and were set to 0 in our simulations for that given timepoint. We simulate each combination 100 times and take the mean temporal variability in population dynamics, estimated using both  $d$  and  $cv$ . All populations were initiated with 50 individuals and run for 100 timesteps.

Variation in growth rate ( $\sigma_R$ ) was more important for temporal variability in population dynamics than variation in competitive effects ( $\sigma_\alpha$ ) given the range of parameter space we examined (Figure S2). This leads to the intuitive suggestion that population dynamics will be more variable in more temporally variable environments. This has a known theoretical basis (Tuljapurkar, 2013), though acclimation and trait-based responses have resulted in mixed evidence for this in natural (Le Coeur et al., 2022) and experimental (Kremer et al., 2018) populations. For a much more complete theoretical treatment of the effects of environmental variation (including autocorrelated environmental variation) on population dynamics, see the text of (Tuljapurkar, 2013) and previous work (Tuljapurkar, 1982, 1989).

**The variable effects of environmental variation** Interestingly, the effects of temporal variation in environmental conditions – modified by incorporating temporal variation in demographic parameters  $R$  and  $\alpha$  – resulted in different amounts

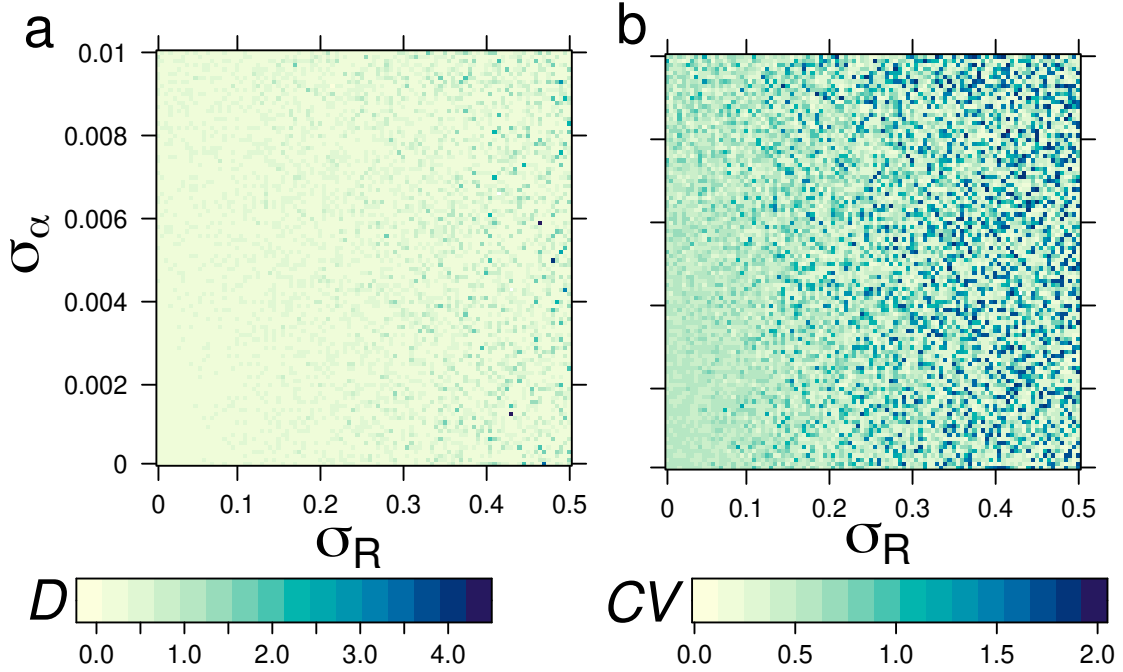


Figure S2: Temporal variability – quantified using  $D$  (panel a) and  $CV$  (panel b) – was related to unstructured temporal variation in population growth rate  $\sigma_R$ , but not strongly related to the variation in density-dependent competition  $\sigma_\alpha$  based on Ricker model simulations. This suggests that environmental gradients influencing population growth rates will likely lead to more variable population dynamics.

of variation in temporal variability estimates, with the variability in the  $D$  statistic increasing with variation in population growth rate  $R$  (Figure S3), suggesting that more variable growth rates resulted in more variation in the resulting estimates of population variability. This was not as evident when temporal variability in population dynamics was estimates using  $CV$ , potentially due to the differences between  $D$  and  $CV$ , as  $D$  considers the structure of the time series while  $CV$  does not. Generally, these two measures tend to be quite related (Figure S5).

**Temporal variability in population dynamics as a function of shifts to mean and temporal variability in population growth rates** Species identity was the most important predictor of temporal variability in population dynamics in the NEON beetle data relative to site and environmental variability.

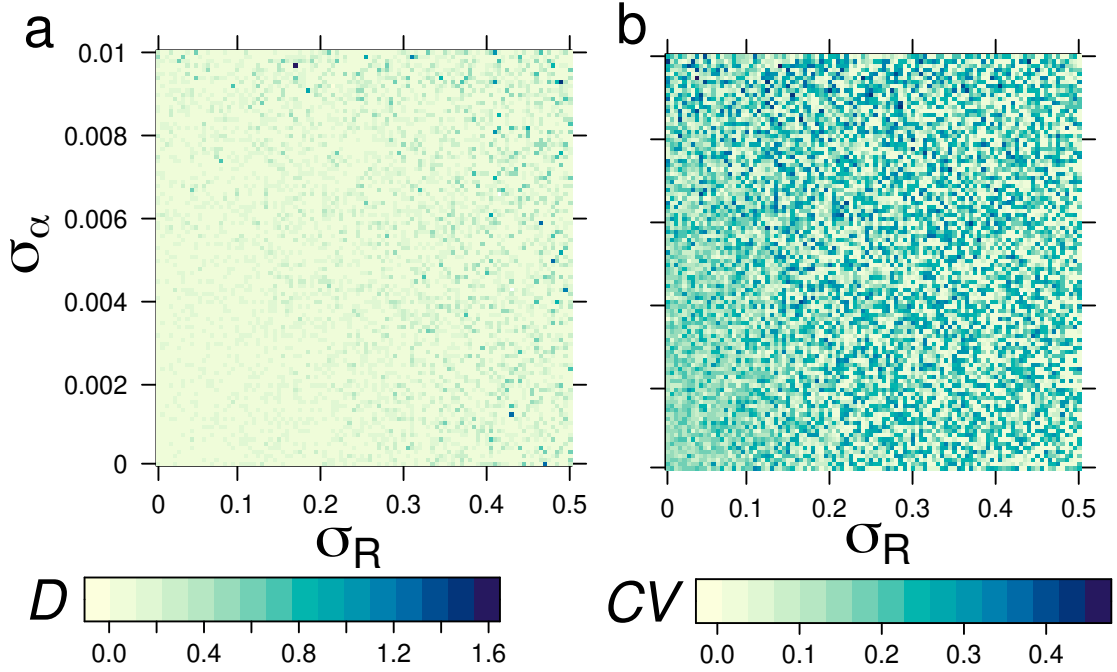


Figure S3: The variation among replicate simulations in temporal variability – quantified using  $D$  (panel a) and  $CV$  (panel b) – was weakly related to unstructured temporal variation in population growth rate  $\sigma_R$ , but not strongly related to the variation in density-dependent competition  $\sigma_\alpha$  based on Ricker model simulations. Differences in the two measures of temporal variability may be the underlying driver, as the  $D$  statistic considers the structure of the time series, while  $CV$  is agnostic to the temporal structure of the time series.

Here, we explore how this relates to simulated population dynamics by considering species differences to be differences in mean population growth rate, and environmental variability as the temporal variability in population growth rates. For these simulations, we explored across a range of population growth rates ( $R = [0.75 - 2.5]$ ), with temporal variability in population growth rate ( $\sigma_R$ ) drawn from a normal distribution with mean  $R$  and standard deviation between 0 and 0.5. For each combination of 100 values between these bounds, we simulated Ricker population dynamics 100 times for 100 timesteps, estimated temporal variability as  $D$  and  $CV$  and took the mean value.

Both mean population growth rate  $\bar{R}$  and temporal variability in population

growth rate  $\sigma_R$  influenced the resulting temporal variability in population dynamics (Figure S4). Reinforcing our previous finding in Figure S1, temporal variability in population dynamics decreased with increasing mean population growth rate  $\bar{R}$ , and more temporal variability in  $R$  increased temporal variability in population dynamics (Figure S4). This suggests that even in the case where there is no environmental variability, differences in mean population growth rates could underlie the importance of species identity on resulting temporal variability in population dynamics.

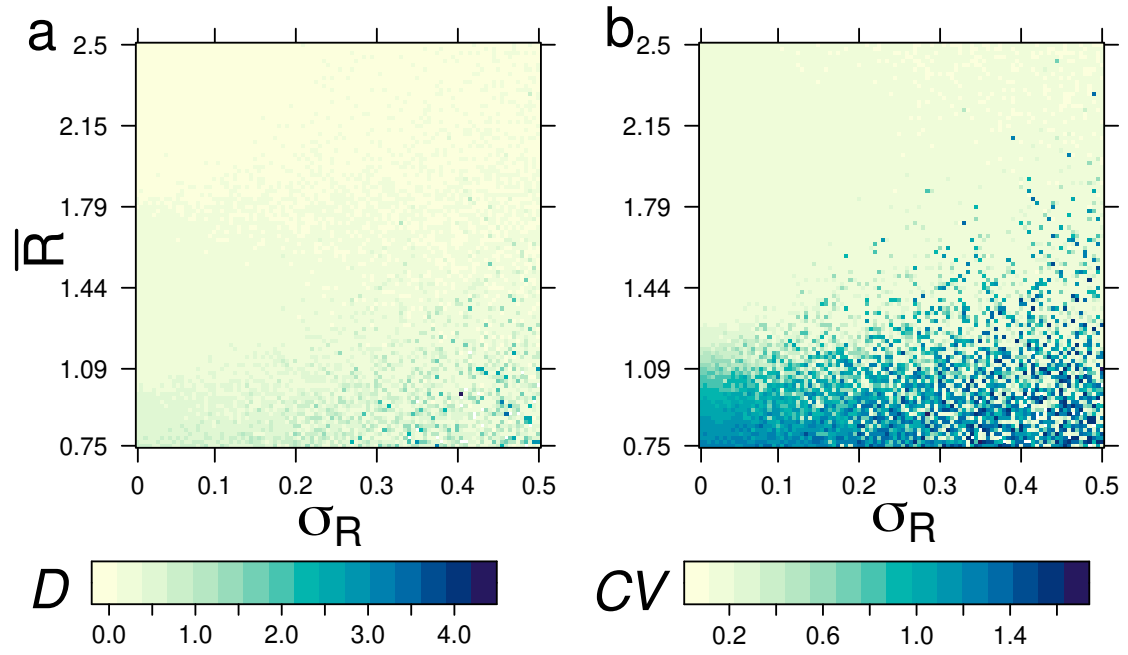


Figure S4: The variation among replicate simulations in temporal variability – quantified using  $D$  (panel a) and  $CV$  (panel b) – was negatively related to mean population growth rate ( $\bar{R}$ ) and positively related to temporal variability in population growth rate  $\sigma_R$ . This suggests that species differences in mean population growth rates and environmental effects leading to temporal variability in population growth rates away from a mean can both influence temporal variability in population dynamics.

## The importance of *how* temporal variability was estimated

In the main text, we use the  $D$  statistic as a measure of temporal variability. Here, we explore how using a measure which is agnostic to the temporal order of events influences our overall findings. These two methods of estimating temporal variability resulted in related measures (Figure S5). Further, the existence of the phylogenetic signal persisted when estimating temporal variability as the coefficient of variation ( $k = 0.312$ ,  $p = 0.002$ ,  $\lambda = 0.379$ ,  $p < 0.0001$ ; Figure S6).

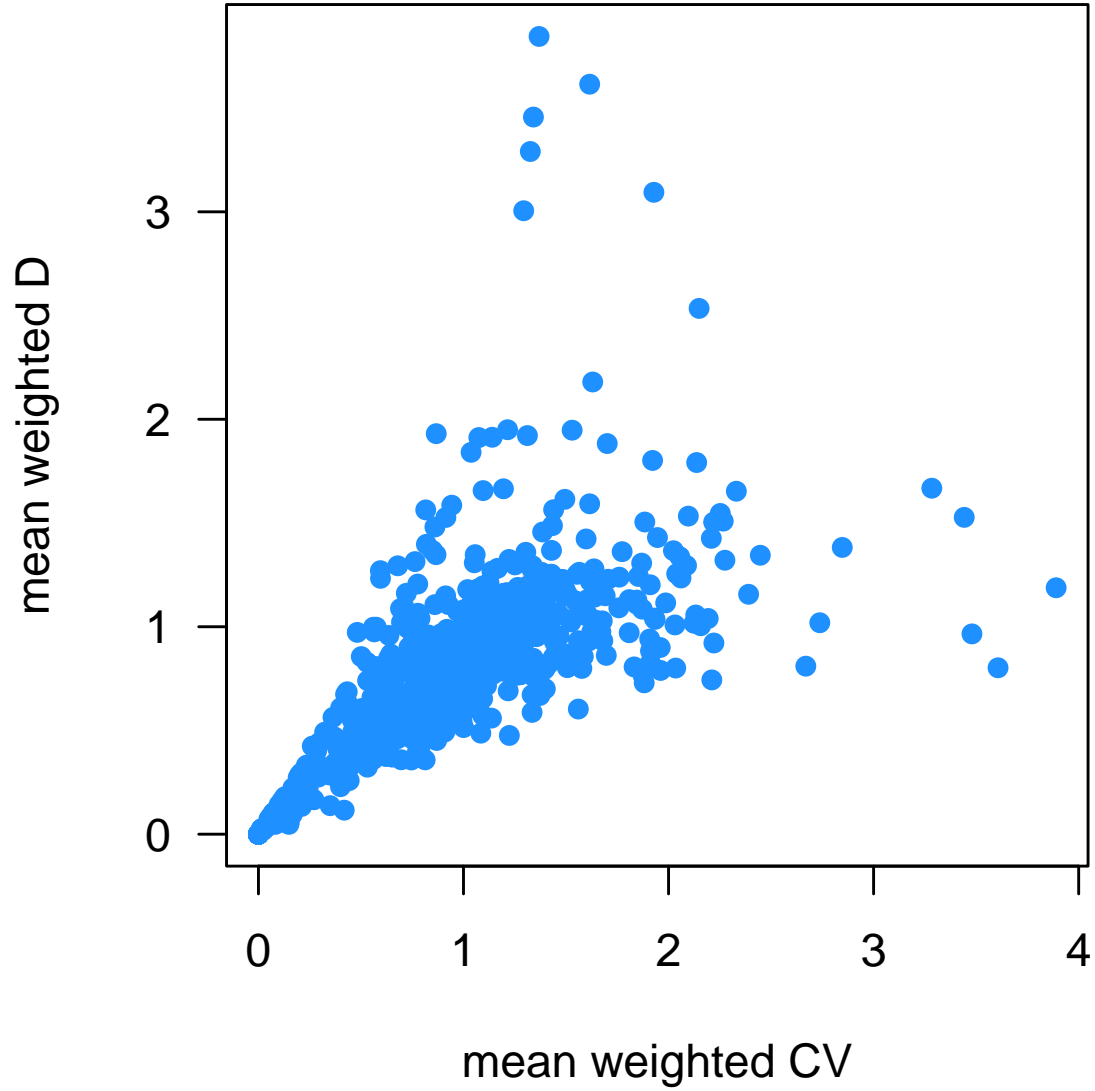


Figure S5: The two measures of temporal variability considered here – the  $D$  statistic and the coefficient of variation ( $CV$ ) – were positively related to one another. Each point represents a species and site combination, meaning that widespread species will be represented by multiple points, just as species-rich sites will correspond to multiple points.



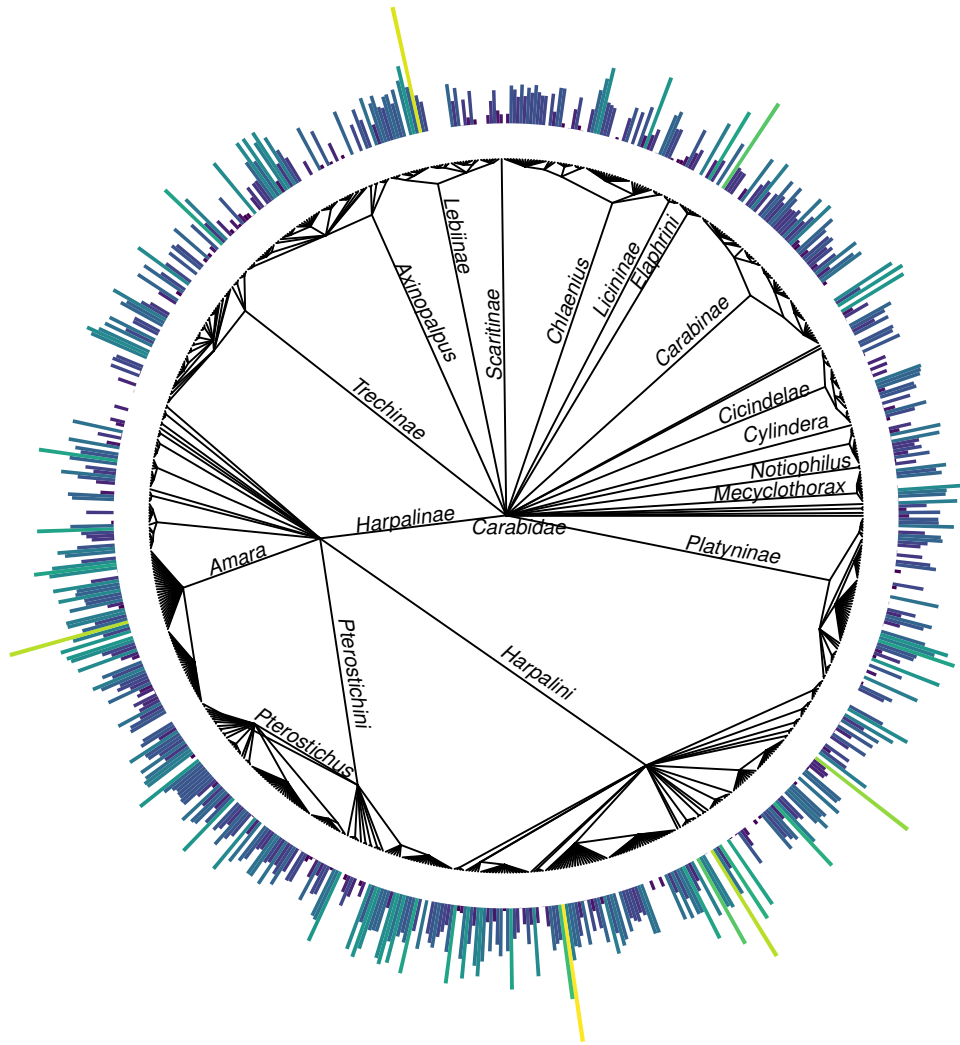


Figure S6: The distribution of mean temporal variability (coefficient of variation weighted by the number of sampling events per site) across the ground beetle phylogeny. Species with especially high temporal variability included *Harpalus reversus*, *Pasimachus obsoletus*, and *Discoderus beauvoisii*.

## **Attempting to remove the influence of seasonality**

We estimated temporal variability using the entire time series, though we recognize the potential influence of seasonality on resulting estimates. That is, species phenology in terms of reproductive timing and peak abundance may influence temporal variability, as species may have seasonal abundance peaks. These peaks likely – though not certainly – adhere to the annual seasonal timescale. We were concerned that one aberrant year could bias estimates of temporal variability. We explore this by estimating temporal variability of species for each year at each site they were found. We then compared the mean annual temporal variability to our composite estimate of temporal variability, finding a positive relationship between the two estimates (Pearson’s correlation = 0.542,  $p < 0.0001$ ; Figure S7). Further exploration of population dynamics is still warranted, as changing climate and directional changes in annual abundance over the sampling period may provide interesting insight into species population dynamics in the face of a changing climate.

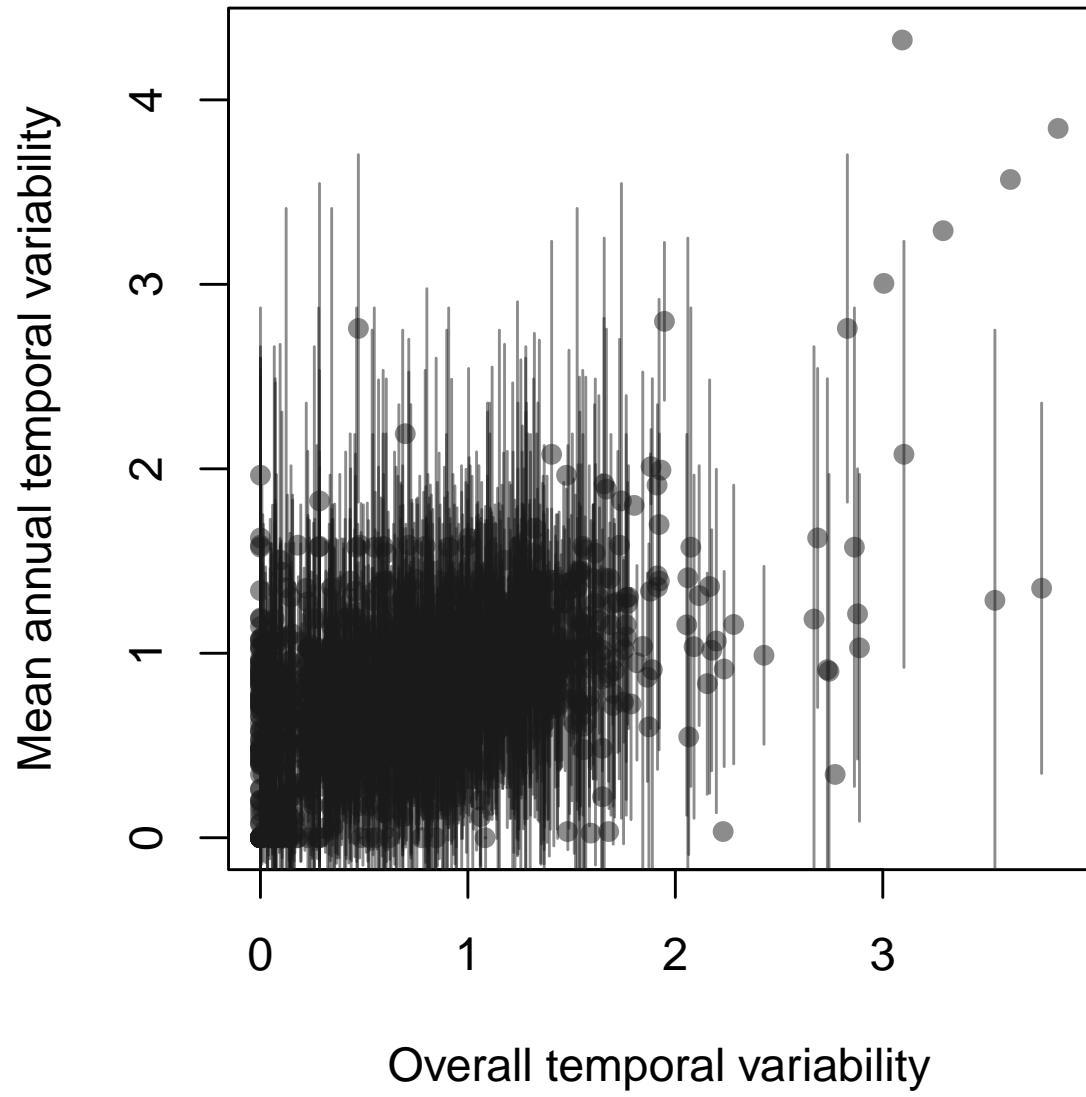


Figure S7: Mean annual temporal variability (error bars are  $\pm 1$  standard deviation) was positively related to temporal variability estimated using the entire sampling period.

## **The influence of the number of sampled sites and beetle ranges**

There is some concern that the geographic distribution of sampling sites may influence the resulting influence of geographic location on temporal variability. That is, endemic species to a single site make it difficult to parse out the effects of geographic location of the site from the importance of species identity. However, the average number of sites where beetle species were found was just over three sites (Figure S8). Given the systematic and long-term sampling of beetles at the community level in the NEON data, we believe our overall findings would not be strongly affected by the inclusion of more sites within the species geographic range. However, fine scale monitoring at species range margins and interior would provide clearer tests of species dynamics across spatial gradients.

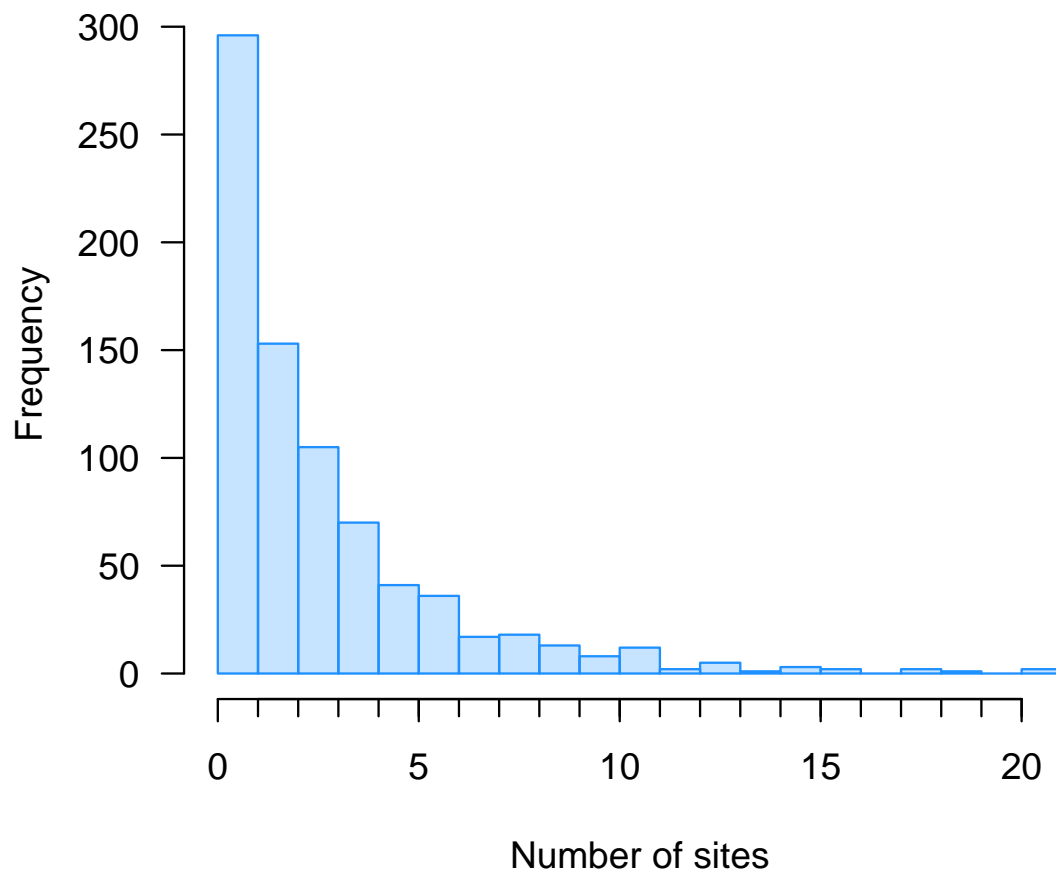


Figure S8: The distribution of the number of sites where each beetle species was found, highlighting that the majority of species were found in quite few sites (around 3 on average), but some were found in upwards of 20 or more locations.

## **Collinearity between space and environment**

Spatial autocorrelation in environmental conditions is a constant spectre in any biogeographical analysis, leading to many muddled associations between latitudinal gradients and aspects of species such as body size or geographic range size, when the underlying driver is not likely to be latitude itself. But we are complicit, as we included both latitude and longitude in our models alongside of estimates of environmental variability. These different groups likely contain some of the same variation, which we can start to tease apart by considering our different composite submodels and the combination models, but collinearity is still an issue. Here, we explore this collinearity between geographic coordinates and our estimates of environmental variability, finding little evidence that environmental variability is spatially structured in our sampling sites (Figure S9). Of course, this would likely be very different if we considered mean environmental variables, as our supplemental models explore. However, we did observe mean-variance scaling in our climatic variables (Figure S10) as well, which contributed to our decision to use climatic means and variability values in separate models.

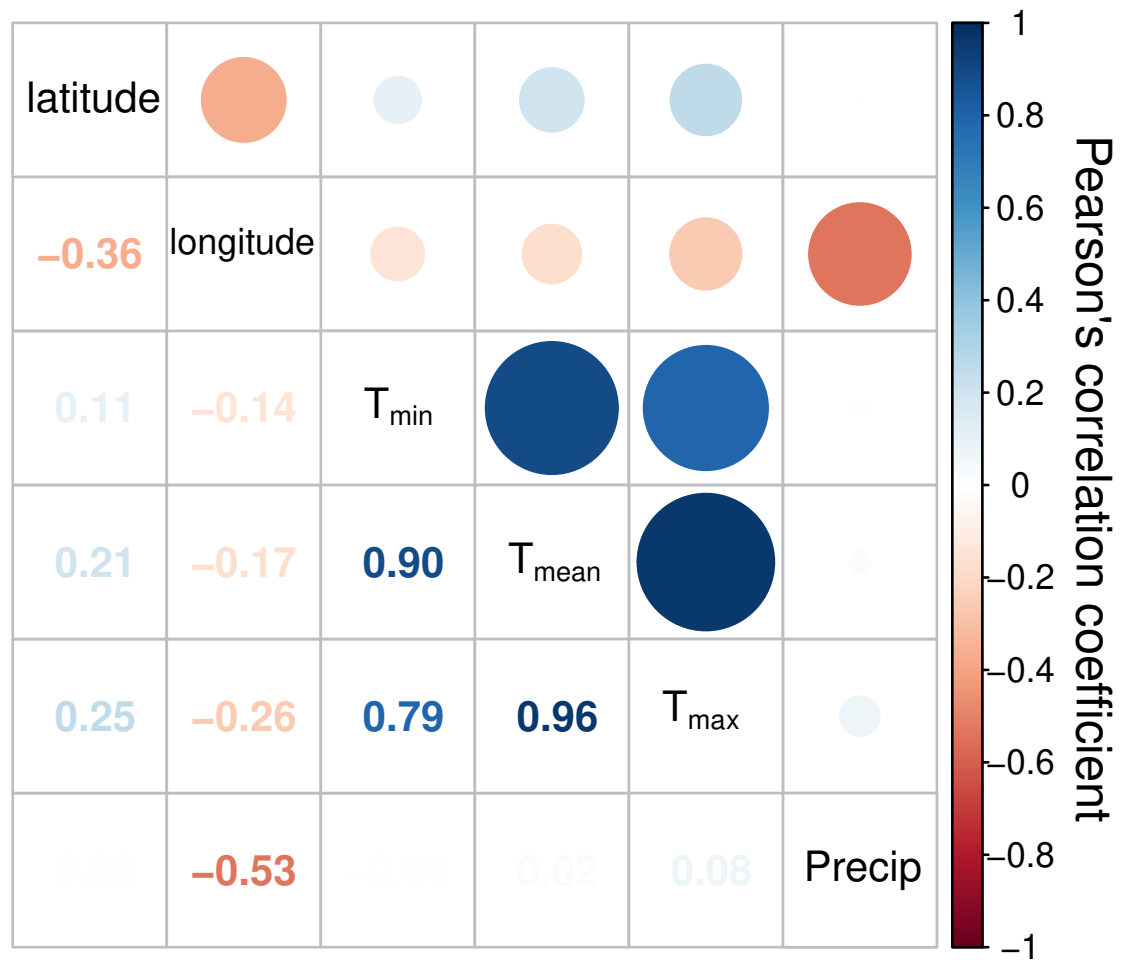


Figure S9: Pearson's correlations between all geographic and environmental variability estimates used in our models of beetle temporal variability. Latitude and longitude were only weakly correlated to environmental variability, but environmental variability estimates of different temperatures were quite positively correlated.

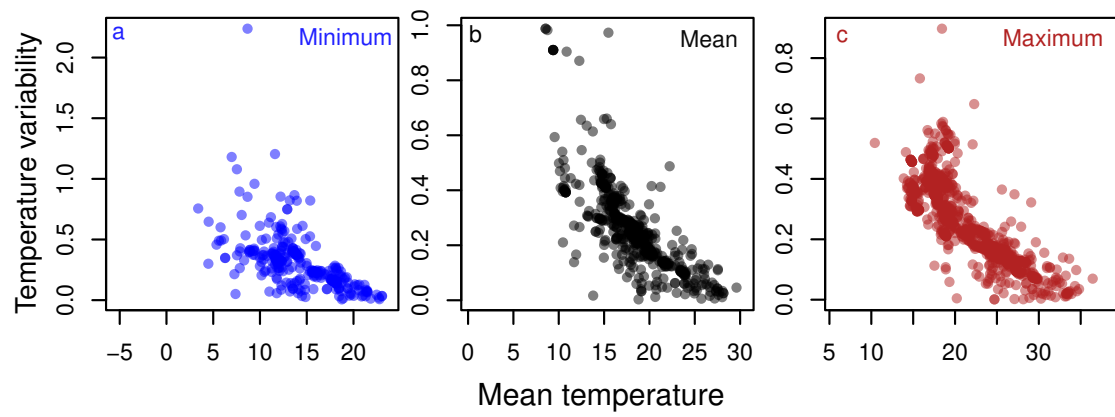


Figure S10: The mean and variance in climatic conditions were strongly related for the minimum temperature (a), mean temperature (b), and maximum temperature (c). This was also true for precipitation (not plotted, but Pearson's correlation of -0.38,  $p < 0.0001$ ).



## Considering mean environmental conditions instead of environmental variability

In the main text, we related temporal variability in beetle population dynamics to environmental variability. Here, we explore the role of mean environmental conditions, highlighting the potential role of different environments to influence population dynamics in the absence of temporal variation in the environment (i.e., demographic rates that are a function of temperature could produce more variable population dynamics as a function of mean temperature independent of any variability around the temperature). We find that the inclusion of mean environmental conditions does not improve model performance in the environment submodel (adjusted  $R^2 = 0.0098$ ), and actively degrades model performance in composite models relative to the models incorporating environmental variability (Figure S11).

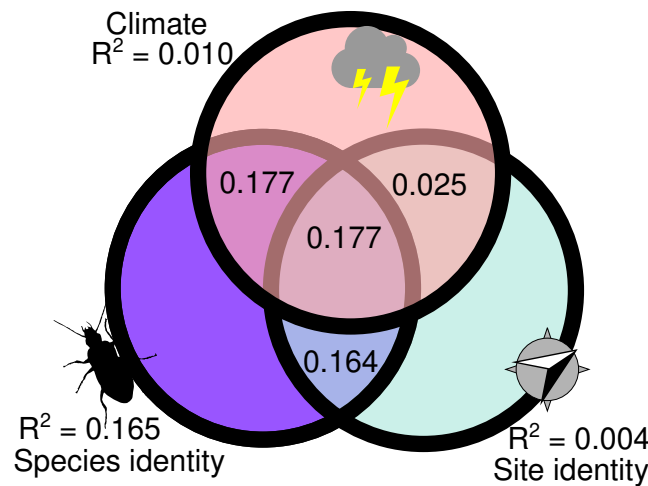


Figure S11: Adjusted  $R^2$  values for each submodel containing different combinations of geographic location (latitude and longitude of site; lower right component), environment (mean temperature and precipitation; top component), and species identity (lower left component) on temporal variability. For instance, the model containing geographic location and environment is the overlapping region in the top and right circles, and this model had an adjusted  $R^2$  value of 0.025.

We also wanted to explore the relationship between mean and variability in environmental conditions. These two may be related, as spatial variation in environments may promote a negative relationship between mean and variability in environmental conditions. For instance, the tropics represent a higher mean temperature, but tend to have less temporal variation in temperature, just as more temperate locations may have lower mean temperature, but display pronounced seasonality in temperature. We find that this is generally true in our restricted sampling sites, as the NEON sampling sites considered here were mostly in North America (Figure S12).

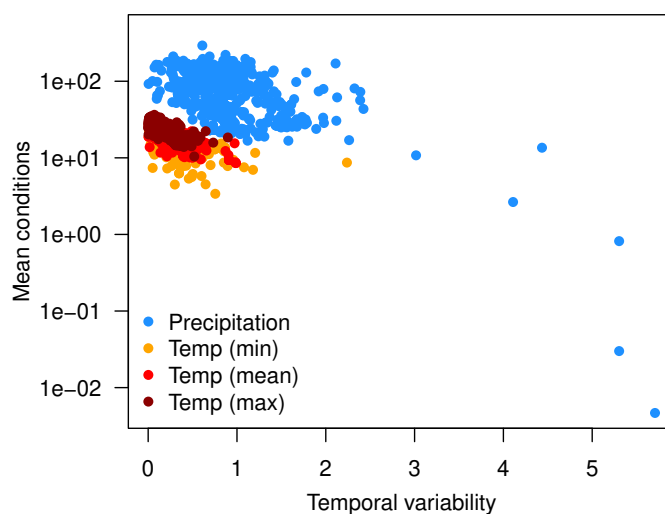


Figure S12: The relationship between environmental variability ( $x$ -axis) and mean environmental conditions ( $y$ -axis; log-scaled).