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RESEARCH

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 USA 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.

Keywords Temporal variability · Population dynamics · Ecological time series · NEON

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 are 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 (Breton and Addicott 1992; Hudson et al. 1992; Brännström and Sumpter 2005). 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 (Tuljapurkar 1982; Bjørnstad and Grenfell 2001; Lundberg et al. 2000; Boyce et al. 2001). 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

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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 USA 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; Niemelä 2001; Marrec et al. 2017). 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 USA (Kao et al. 2012) (see Fig. 1a for the spatial distribution of

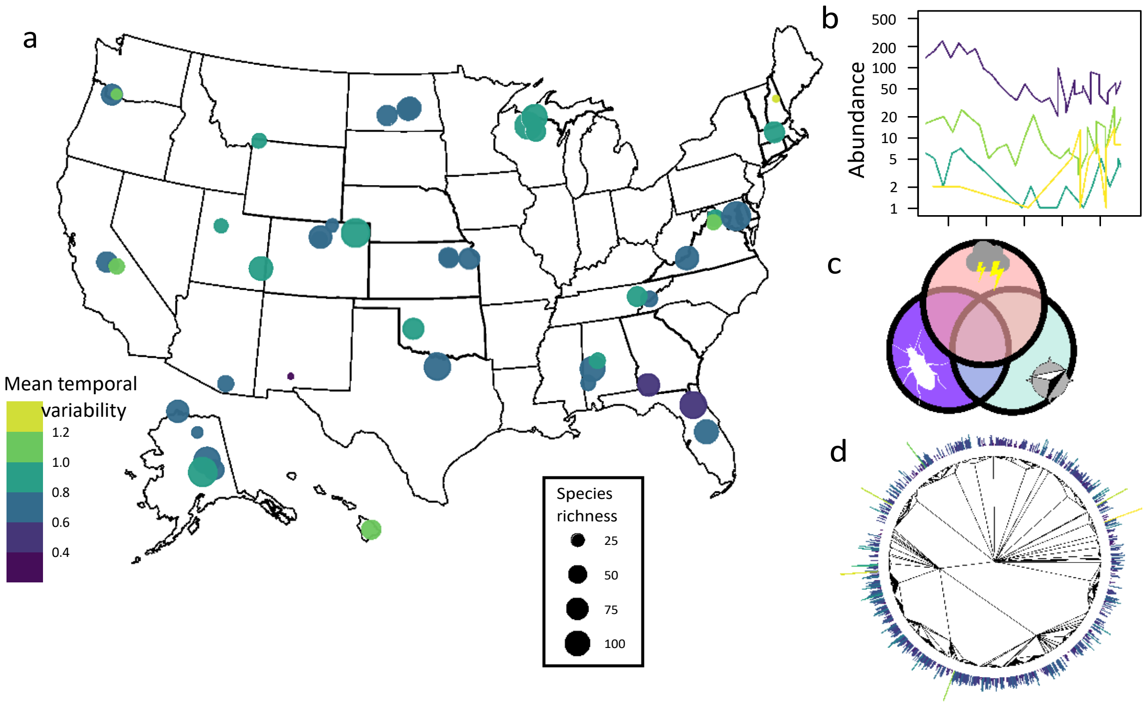

Fig. 1 The spatial distribution of carabid beetle sampling sites across the USA (**a**), where point size is proportional to the overall species richness in the site, and color is proportional to the mean temporal variability estimate. Using these time series data on species abundances (**b**), we estimated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

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 2 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 four pitfall traps, roughly 20 m 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 the 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 (Tuljapurkar 1982, 1989; Kremer et al. 2018; Ovaskainen and Cornell 2006).

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 Eq. 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 (Fig. S1), low temporal variability in population growth rates (Figs. S2–S4), and not strongly influenced by temporal variation in intraspecific competition (Fig. 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

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

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 seven 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 (Fig. 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 and *K* statistics, computed using the `phytools` R package (Revell 2012).

R code and data to reproduce the analyses are 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 (= 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 (= 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 (Fig. 2). These findings were very similar when considering mean environmental conditions instead of environmental variability (see Supplemental Materials).

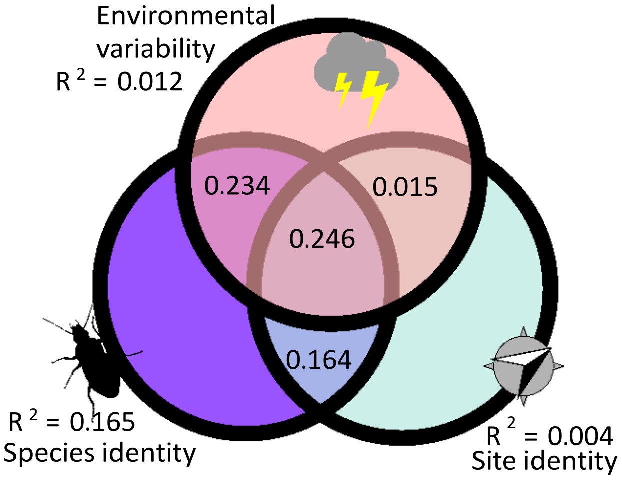

Fig. 2 Adjusted R^2 values for each submodel containing different combinations of geographic location (latitude and longitude of site; lower right component), environment (variability in monthly temperature and precipitation; top component), and species identity (lower left component) on temporal variability. 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

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 Supplemental Materials). 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 (Fig. 3). Both approaches found a significant phylogenetic signal in weighted mean temporal variability (= 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 the 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, $p < 0.0001$).

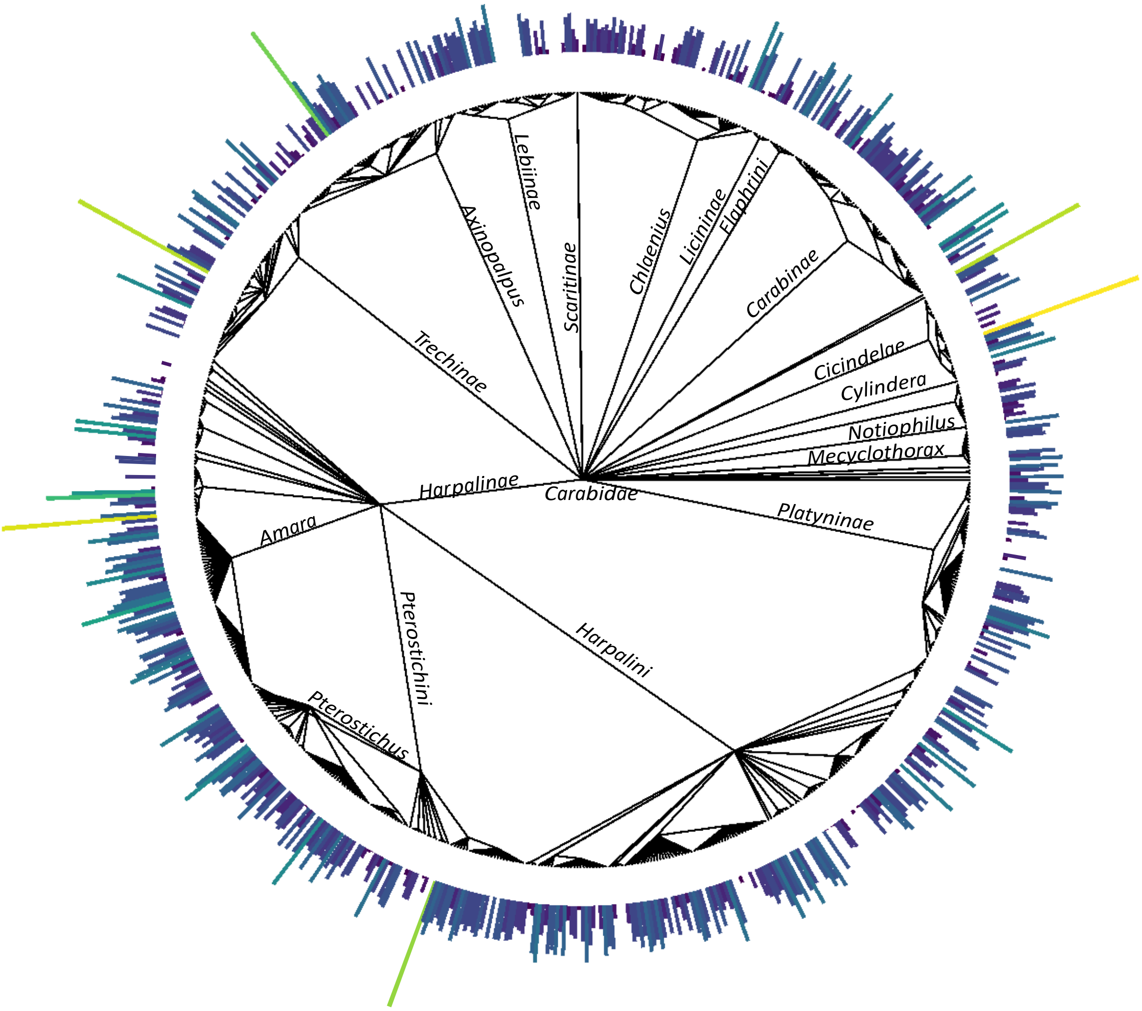

Fig. 3 The distribution of mean temporal variability (*D* statis-tic weighted by the number of sampling events per site) across the ground beetle phylogeny (height and color of bars correspond to mean temporal variability for a given species). Species with especially high temporal variability included *Cicindela abdominalis*, *Bembidion ampliatum*, and *Calosoma wilcoxi*

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 USA, 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 a 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 Fig. 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 >100 km 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 the 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 (Melbourne and Hastings 2008; Dallas et al. 2021), and this is an important and challenging next step for understanding fluctuating population dynamics in natural populations.

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Data availibility *R* code is available on figshare at https://doi.org/10.6084/m9.figshare.21217709. The NEON data should be cited directly if used, as NEON (National Ecological Observatory Network). Ground beetles sampled from pitfall traps, 2013–2021. https://doi.org/10.48443/tx5f-dy17. Dataset accessed from https://data.neonscience.org.

Declarations

Competing interests The authors declare no competing interests.

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