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Incorporating the temporal autocorrelation of demographic rates into structured population models

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Population dynamics are typically temporally autocorrelated: population sizes are positively or negatively correlated with past population sizes. Previous studies have found that positive temporal autocorrelation increases the risk of extinction due to 'inertia' that prolongs downward fluctuations in population size. However, temporal autocorrelation has not yet been analyzed at the level of life cycle transitions. We developed an R package, colorednoise, which creates stochastic matrix population projections with distinct temporal autocorrelation values for each matrix element. We used it to analyze long-term demographic data on 25 populations from the COMADRE and COMPADRE databases and simulate their stochastic dynamics. We found a broad range of temporal autocorrelation across species, populations and life cycle stages. The number of stage-classes in the matrix strongly affected the temporal autocorrelation of the growth rate. In the plant populations, reproduction transitions had more negative temporal autocorrelation than survival transitions, and matrices dominated by positive temporal autocorrelation had higher extinction risk, while in animal populations transition type was not associated with noise color. Our results indicate that temporal autocorrelation varies across life cycle transitions, even among populations of the same species. We present the colorednoise package for researchers to analyze the temporal autocorrelation of structured demographic rates.

Keywords: colored noise, environmental reddening, environmental stochasticity, matrix population models, temporal autocorrelation

Introduction

Demographic population models are important both for developing ecological and evolutionary theory and for forecasting population dynamics of threatened and economically interesting populations. Natural populations are subject to environmental variation that profoundly affects their dynamics, which is why modelers often account for this variation in order to make accurate forecasts (Lande et al. 2003, Ovaskainen and Meerson 2010). Accounting for environmental variation is usually done by including random variation in demographic rates with the assumption of white noise.

White noise is random noise where demographic rates or the environment driving demographic rates are uncorrelated to their values at previous time points. However, the assumption of white noise is unrealistic, as most environmental variation exhibits colored noise dynamics. That is, time series have a 'memory' where the environment at each time point is influenced by the ones that came before it (Vasseur and Yodzis 2004). Moreover, previous studies that do incorporate colored noise typically do not consider that different demographic rates may differ in autocorrelation (but see Morris and Doak 2002).

The terminology of noise color comes from the mathematical formulation of temporal autocorrelation, which can either be described as the covariance of values in the series with values preceding them at a given lag time (Kendall 1976) or as the sum of sine waves with random wavelength (Halley 1996). In the former case, white noise is represented by zero covariance, red noise by positive covariance, and blue noise by negative covariance. In the latter case, white noise is represented by random sine waves of equal amplitude, red noise consists of sine waves whose amplitudes are positively related to wavelength, and blue noise consists of sine waves whose amplitudes are negatively related to wavelength. Colored noise in demographic rates may reflect the autocorrelation of environmental drivers, resulting in red noise if favorable (unfavorable) years tend to follow favorable (unfavorable) years, and blue noise if favorable and unfavorable years tend to alternate. Colored noise could also result from within-population processes such as mast seeding in plants or collective behavior in animals leading to among-individual synchrony in resource allocation.

Effects of temporal autocorrelation on population dynamics have been investigated in simulated, empirical and theoretical studies. Simulation approaches are common, likely because temporal autocorrelation is difficult to measure from real data; long time series are required to calculate the autocorrelation accurately (Kendall 1976). Many simulation studies, including simple counts of population size (Halley and Kunin 1999), diffusion models with density dependence (Foley 1994), Turchin and larva–pupa–adult models (Greenman and Benton 2003), and cellular automata models (Mustin et al. 2013), have all found that red noise increases extinction risk under most conditions. This makes intuitive sense, as positive temporal autocorrelation creates inertia in population dynamics such that when a population reaches a decline, it is likely to stay in decline. In contrast, blue noise may have an overall stabilizing effect on populations, because a downward fluctuation is likely to be followed by an upward one. An investigation of the Global Population Dynamics Database (2010) revealed that the majority of populations with sufficient data had positive autocorrelation in their growth rates, though some were strongly negative as well (Ferguson et al. 2016).

For the most commonly used type of structured population models, the matrix projection model (MPM), several studies have confirmed that positive environmental autocorrelation tends to increase extinction risk, confirming findings from simpler population models (Heino and Sabadell 2003, van de Pol et al. 2011, Paniw et al. 2018). Tuljapurkar and Haridas (2006) formulated a sensitivity measure of population growth rate to autocorrelated variability, and showed that temporal autocorrelation may in some cases have stronger effects on growth rates than environmental stochasticity. However, we still lack studies on the noise color of the individual matrix elements that determine the population growth rate in MPMs (but see Morris and Doak 2002). Thus, we neither know much about how noise colors of matrix elements may vary nor the effects of such variation on population projections.

Here we model structured populations parameterized using real data while taking the temporal autocorrelation of each matrix element into account. First, we measure the temporal autocorrelation of matrix elements for species in the COMADRE and COMPADRE databases of projection matrices (Salguero-Gomez et al. 2015, 2016) for which there are sufficient data. Second, we parameterize MPMs using these data to investigate how autocorrelation in matrix elements influences autocorrelation in the stochastic population growth rate. Third, we manipulate the stage-class dimensions of the matrices and compare the model results. Fourth, we assess how projected population trajectories and extinction risks change when we shift from an assumption of white noise in matrix elements to including the observed autocorrelation values.

We asked the following four questions: 1) does noise color differ between survival and fertility elements in matrices? We could expect such a difference if one of these transition types are under stronger selection to vary in a certain way. One selection pressure affecting survival and fertility differently could be the effect of seed predators; if blue noise in plant fertility reduces seed predation because it makes the seeds a less reliable resource (Herrera et al. 1998). Differences between survival and fertility elements may also occur due to a stronger sensitivity to environmental variation in one type of element, or due to statistical artifacts (cf. Morris and Doak 2004, Bjorkvoll et al 2016). 2) Is the noise color of the stochastic growth rate associated with the noise color of the matrix elements to which the growth rate is most sensitive? 3) Is the noise color of the stochastic growth rate affected by the stage-class dimensions of the matrix? We expect such effects because stage-class dimensions of matrices are known to affect demographic rates (Salguero-Gomez and Plotkin 2010). 4) Will population trajectories be more variable, and therefore extinction risk higher, in stochastic matrix models where red noise matrix elements predominate than in stochastic models that assume white noise (and the reverse for models where blue noise matrix elements predominate)?

We also present the R package colorednoise where the noise color of matrix elements can be specified and included in stochastic population projections.

Methods

The colorednoise R package

To create stochastic matrix population models which incorporate the temporal autocorrelation values of each matrix element, we developed the colorednoise package (<http://cran.r-project.org/package=colorednoise>) in R ver. 3.5.0 (<www.r-project.org>). The package can generate colored noise for any autocorrelation value, measure the temporal autocorrelation of a time series with a bias correction for short time series, and run stochastic population models. These population models can be unstructured or structured, with specified temporal autocorrelation values for each matrix element. For structured populations, the user can add information about the covariance among matrix elements. The package does not support density-dependent models at this time. See Supplementary material Appendix 1 for more details on the package's functionality.

Data

Matrix population models contain information about how individuals on average transition among discrete classes over a given time step. Classes are often based on age, life cycle stage or size and the time step used is often one year. Each matrix element consists of a mathematical combination of the underlying vital rates: fertility and survival, and for stage- and size-based matrices the probability of transitioning to (or remaining in) a particular class.

We used published matrices extracted from the COMADRE and COMPADRE databases of population matrices (Salguero-Gomez et al. 2015, 2016), filtered on four criteria. We chose populations with matrices created on one-year intervals for fifteen continuous years or more, because even with the bias correction in our autocorrelation estimation method, estimates of autocorrelation become imprecise for short time series. We required both survival (or in stage-classified matrices 'survival-growth') and fertility data, and rejected simulated populations. We also excluded matrices that were averaged or pooled across different populations.

The populations that met our criteria include 10 species of perennial forb, one cactus, seven primates, two other mammals and one bird (more details in Table 1). Most of the animal populations were long-lived and most of the plant populations were short-lived. Four of the plant population matrices were size-based and three of the animal populations were stage-based; the rest were age-based (Supplementary material Appendix 1 Table A1). The sample sizes for the populations we chose were substantial, ranging from 417 to 3487 individuals in the plants, and 167 to 3592 individuals in the animals. The primate matrices all included repeated elements – since the researchers did not have data on survival rates for every age class, the values for survival elements were repeated across some age classes, thus the temporal autocorrelation for these elements was identical.

None of the studies included data on structured vital rates year by year, so we analyzed matrix transitions instead of the underlying vital rates. The 'fertility' elements thus contain information about both fertility and survival (either of the mother or the offspring, depending on if data was collected in a pre- or post-breeding census, cf. Morris and Doak 2002). In plants, the 'survival' in fertility elements also includes the probability of germination. Similarly, the non-fertility, 'survival' elements of the stage-based matrices contain information about both survival and growth (where 'growth' can also be stasis or retrogression). The fact that we did not analyze patterns at the underlying vital rate level means that differences in noise color among survival and fertility rates may be more extreme than what is evident from the matrix elements, if the survival rate and the fertility rate underlying the fertility matrix elements have the opposite noise color.

Analysis

Matrix models can be used to project population dynamics; by multiplying matrices with vectors containing the number of individuals in each class, a new vector describing the population next time-step is produced (Caswell 2001). Deterministic matrix models, based on a single matrix, will converge to a stable population growth rate (and a stable population structure). Stochastic population growth, accounting for among time-step variation in matrix elements, is typically simulated by repeating matrix multiplications with either entire matrices drawn at random from the set of observed matrices at each time-step, or by letting matrix elements vary randomly (or with some constraint due to their covariation among matrix elements). This would correspond to white noise. When we model effects of colored noise, it is the color of the noise of each matrix element observed over time that we account for. That is, we do not investigate autocorrelation in single individuals, but in average demographic rates of all individuals in the population across time.

For comparing stochastic simulations across each qualifying species we built matrices based on randomly varying vital rates and pooled the juvenile stage-classes for species with high matrix dimensionality so that all matrices were either 2×2 or 3×3 (see Table 2 for the species with pooled stage-classes). We used these reduced matrices to address research questions 2 through 4. We did this to avoid effects of matrix dimensionality influencing the comparisons, as the effects of high matrix dimensionality overwhelmed all other factors when matrices were larger than 5×5 (see Supplementary material Appendix 1 Fig. A1 for the outcomes of simulations where the matrix dimensionality was not modified in the animal species).

Within-year covariance of matrix elements was calculated for all populations except for *Cebus capucinus*, *Gorilla beringei* and the northern resident population of *Orcinus orca*, whose covariance matrices were not positive definite (that is, there was some issue with the data, making the covariance among two or more matrix elements inconsistent with their

Table 1. Variance in final population sizes in white noise and colored noise matrix model simulations.

Population	Common name	Life expectancy	Sample size	Years	Stages	Fertility noise color	Survival noise color
Plants							
Cirsium undulatum	gray thistle	1.33	632	30	2	−0.181	0.072
Echinacea angustifolia	blacksamson Echinacea	1.65	417	31	2	−0.219	0.072
Paronychia jamesii	James' nailwort	1.33	l064	33	2	−0.222	0.690
Pediocactus bradyi A	marble canyon cactus	6.80	1049*	22	5	−0.085	0.021
Pediocactus bradyi B	marble canyon cactus	7.42	1049*	22	3	0.297	0.347
Pediocactus bradyi C	marble canyon cactus	12.75	1049*	22	3	0.502	0.050
Pediocactus bradyi D	marble canyon cactus	15.44	1049*	22	3	0.279	0.012
Physaria ovalifolia	roundleaf bladderpod	2.27	1064	28	2	−0.149	0.199
Psoralea tenuiflora	scurfy pea	1.20	3487	33	2	−0.033	0.283
Ratibida columnifera	prairie coneflower	0.82	844	29	2	−0.042	0.320
Solidago mollis	velvety goldenrod	1.06	2144	30	2	−0.179	0.746
Sphaeralcea coccinea	scarlet globemallow	1.03	971	55	2	−0.076	0.510
Stenatia nigricans	prairie bluet	1.45	731	29	2	−0.056	0.570
Thelesperma megapotamicum	hopi tea greenthread	1.01	608	29	2	−0.036	0.354
Animals							
Callospermophilus lateralis	golden-mantled ground squirrel	1.62	831	18	6	−0.030	0.305
Cebus capucinus	white-faced capuchin	22.37	167	22	8	0.138	−0.255
Cercopithecus mitis	blue monkey	19.92	412	28	9	0.155	0.118
Ciconia ciconia	white stork	39†	3592	28	2	0.074	−0.408
Gorilla beringei	mountain gorilla	45.67	269	42	11	0.656	0.031
Macaca mulatta	rhesus macaque	17.5	2074	24	5	0.084	0.297
Orcinus orca A	killer whale	29.8	740*	24	7	0.211	0.148
Orcinus orca B	killer whale	33.9	740*	24	7	0.009	0.057
Pan troglodytes	chimpanzee	23.22	285	45	17	0.136	0.034
Papio cynocephalus	yellow baboon	19.40	1055	37	8	−0.045	−0.093
Propithecus verreauxi	Verreaux's sifaka	14.27	756	24	8	0486	0.376

Life expectancies are from birth/the first age class, except where indicated that a maximum longevity was drawn from the AnAge database (†). Sample sizes are population-specific and include all individuals sampled throughout the study duration, except where indicated that the study did not specify sample sizes for each population (*). All of the population matrices are female-only (or female reproduction-only in the case of bisexual plants). Fertility and survival noise color are the averaged temporal autocorrelation values for all fertility and survival matrix elements, respectively.

Table 2. Temporal autocorrelation in animal populations with unmanipulated matrices and matrices with pooled age classes.

Population	Unmanipulated autocorrelation	Manipulated autocorrelation
Callospermophilus lateralis	0.112	0.223
Cebus capucinus	0.637	0.222
Cercopithecus mitis	0.678	0.329
Ciconia ciconia	−0.141	NA
Gorilla beringei	0.666	0.340
Macaca mulatta	0.629	0.242
Orcinus orca A	0.000	0.277
Orcinus orca B	−0.236	0.309
Pan troglodytes	0.698	0.249
Papio cynocephalus	0.702	0.276
Propithecus verreauxi	0.630	0.309

The table shows the temporal autocorrelation of the stochastic growth rate in the original animal matrices used, which range in dimensionality from 2×2 to 17×17, and the temporal autocorrelation of the growth rate after the dimensionality was reduced to 3×3. *Ciconia ciconia* matrices were not manipulated because they already had low dimensionality (2×2).

respective covariance with a third element). In simulations, values of matrix elements were constrained so that matrices kept the observed covariance structure (see Supplementary material Appendix 1 for details).

Our simulation technique works by generating colored noise for survival matrix transitions on the logit scale, and for fertility–survival matrix elements on the log scale, and transforming the resulting noise back to the natural scale. This transformation imposes boundedness on survival, restricting it to the {0, 1} interval, which could affect the noise color, especially for very low or very high survival. We tested the effect of boundedness on colored noise by generating pure white noise on the logit scale, transforming it to the natural scale, and measuring the temporal autocorrelation. We found that boundedness skews temporal autocorrelation somewhat negative toward the low and high ends of the interval (Supplementary material Appendix 1 Fig. A2), which means that any estimates of positive temporal autocorrelation in survival elements can be considered conservative. We did not find a statistically significant correlation between the values of survival matrix elements and their temporal autocorrelation (Supplementary material Appendix 1 Fig. A3).

We ran two sets of 10 000 simulations for each population, one set with the real observed temporal autocorrelation values for each matrix element, the other set with the assumption of white noise for all matrix elements. For each population we calculated the stable stage structure of the deterministic mean matrix model and used it as the initial population, to avoid the effects of transient dynamics. For both sets we input the mean value and variance of each matrix element, the covariance matrix if available, and 100 years as the simulation length. We then performed another set of identical simulations, but without the covariance matrices. After the simulation runs, we calculated the stochastic growth rate and the temporal autocorrelation of the growth rate using all 100 years of the simulation.

We investigated our first research question, on whether noise color differs between survival and fertility, by measuring the autocorrelation of the matrix elements for each population employing a bias correction for short time series. For these comparisons, we used the original (non-reduced) matrices.

For the second question, we calculated the stochastic sensitivity and elasticity of the population growth rate to each matrix element using the mean-value matrix for each population and compared the sensitivity values to how overall noise color of population growth rate followed the color of specific matrix elements (Supplementary material Appendix 1 Table A2). We also compared these results to those of the no-covariance simulation runs to learn more about the effect of correlated vital rates on noise color.

We investigated the effect of stage structure on noise color (question 3) by comparing the results of the MPMs for species with reduced matrices to MPMs for the original, larger matrix stage-class dimensions.

For each simulation, we calculated the final population size, the stochastic population growth rate, the autocorrelation of the stochastic population growth rate, and whether the population ever dropped below 5% of the initial population size (quasi-extinction threshold), in order to investigate question 4. Since the study populations varied substantially in life span, which may influence these comparisons, we also assessed the effect of setting the quasi-extinction threshold to 50%. However, this did not substantially alter the results (Supplementary material Appendix 1 Fig. A4).

Results

Noise color of matrix elements

There was a variety of patterns of noise color among matrix elements in the populations studied (Fig. 1). In most matrices, there were both blue noise and red noise elements. In species for which we had data for multiple populations (*Orcinus orca* and *Pediocactus bradyi*), the noise color of matrix elements varied among populations of the same species. In the plant populations, fertility matrix elements had bluer noise than survival matrix elements, while the animal populations exhibited no such pattern (Table 1).

Noise color of the stochastic growth rate

Of the 14 sets of colored noise simulations of plant populations, two exhibited red noise in the stochastic growth rate on average (>0.2 autocorrelation; Vasseur and Yodzis (2004)), 12 exhibited white noise (−0.2 < x < 0.2 autocorrelation), and none exhibited blue noise (<−0.2 autocorrelation). The two populations with average red noise in the stochastic growth rate were both from the species *Pediocactus bradyi*. In the white noise simulations, all of the populations had mean temporal autocorrelation within 0.03 of 0, except for two populations of *P. bradyi* (Fig. 2).

Of the 11 sets of colored noise simulations of animal populations, six exhibited red noise in the stochastic growth rate on average, four exhibited white noise and one exhibited blue noise. In the white noise simulations, the results were the same, except for *Gorilla beringei*, which shifted from red noise to white noise (Fig. 2). In general, noise color shifted toward white in the white noise simulations.

In both the plant and animal simulation sets, there was no relationship between the temporal autocorrelation of the matrix elements weighted by stochastic sensitivity and the realized temporal autocorrelation of the stochastic growth rate (Fig. 3).

In all populations, accounting for observed covariance among matrix elements did not have a strong effect on the temporal autocorrelation of the growth rate, or its relationship with the temporal autocorrelation of matrix elements; the autocorrelation was similar in the set of simulations without specified covariance among matrix elements (Supplementary material Appendix 1 Fig. A5).

Stage structure and noise color

The temporal autocorrelation of the stochastic population growth rate was significantly lower in the primate matrices which were manipulated to have three stages than in the original, unmanipulated matrices with more stage classes (Table 2). This was true in both white and colored noise simulations. In the rodent population and the two orca populations, the manipulated 3×3 matrices exhibited higher temporal autocorrelation of the stochastic growth rate.

Effects on population outcomes

In the plant simulations, there was a positive linear relationship between the temporal autocorrelation of the growth rate and the relative difference in variance of population sizes between the white noise and colored noise simulations; in other words, the higher the temporal autocorrelation, the more variance there was in the colored noise simulations relative to the white noise simulations in each population (Fig. 4). However, this association was much weaker in the animal simulations. Accordingly, in the plant simulations, there was also a positive linear relationship between the temporal auto-correlation of the growth rate and the relative difference in extinction risk between the white noise and colored noise
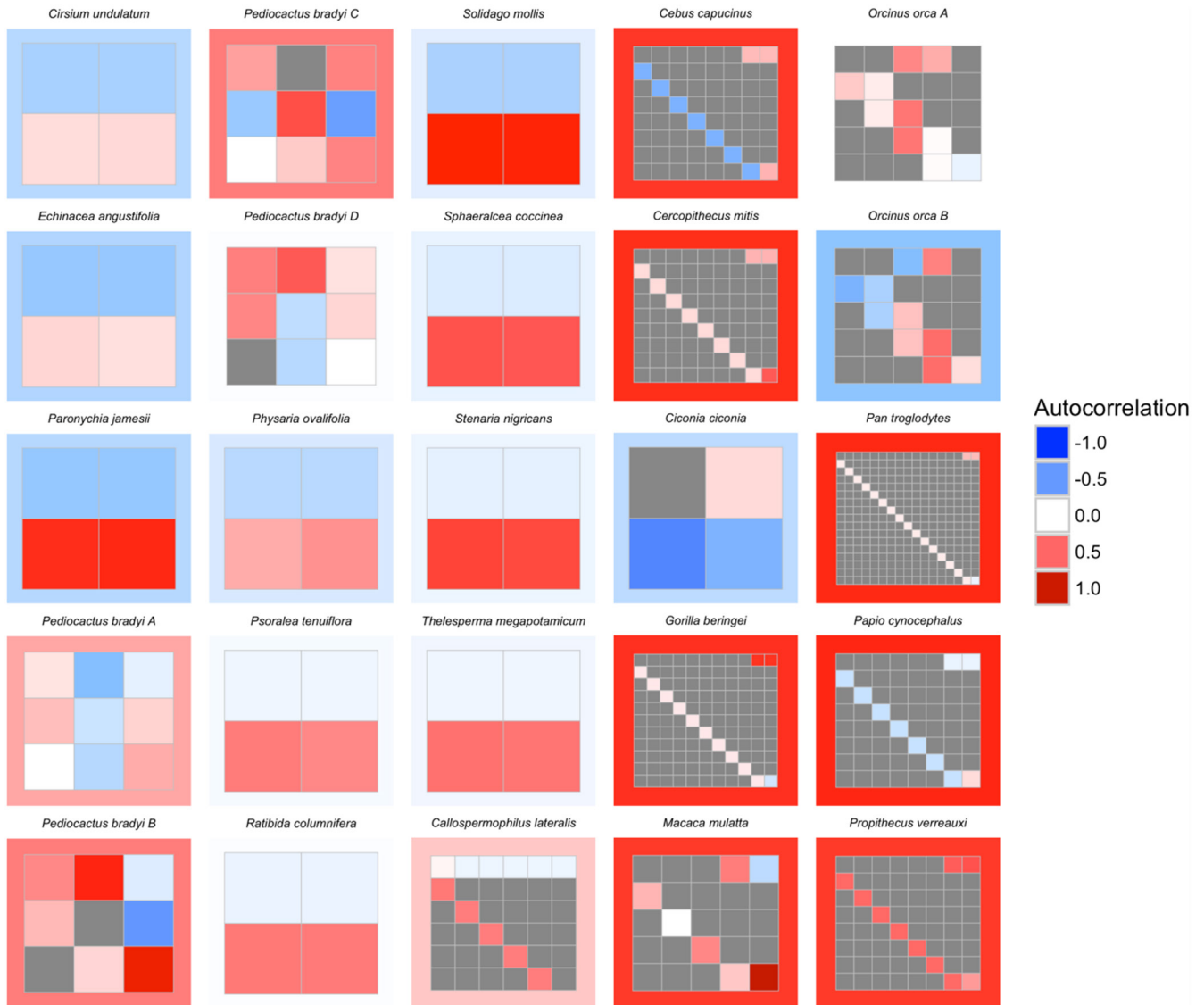
Figure 1. Colored noise in population matrices from COMADRE and COMPADRE databases. Matrices for twenty-five populations drawn from COMPADRE and COMADRE databases, showing the temporal autocorrelation of the elements. The borders around the matrices represent the temporal autocorrelation of the stochastic growth rate averaged across 10 000 simulations incorporating the temporal autocorrelation of the matrix elements. Gray elements are impossible stage transitions, blue elements have negative temporal autocorrelation, red elements have positive temporal autocorrelation and white elements have no temporal autocorrelation. The first 14 populations (the two first columns and the first panel in the third column) are plants, and the remaining 11 populations are animals. Two species have multiple populations: *Orcinus orca* (northern resident killer whales (A) and southern resident killer whales (B)) and *Pediocactus bradyi* (Badger Creek (A), North Canyon east (B), North Canyon west (C) and Soap Creek (D)).

simulations (Fig. 5). None of the animal populations risked extinction in our simulations (defined at a quasi-extinction threshold of 5% of the original population size).

Discussion

We found a broad range of noise color in matrix elements in both plant and animal populations, from strongly blue to strongly red. This result indicates that survival and fertility rates of different life history stages of a population are by

no means guaranteed to have similar temporal autocorrelation. Indeed, in the species where we had access to multiple populations of the same species (*Orcinus orca* and *Pediocactus bradyi*), the noise color of matrix elements varied strongly within the species. We found a link between the stage-class breakdown of a population matrix and the noise color of the stochastic growth rate, and were able to confirm that when red noise matrix elements predominate, extinction risk in stochastic projections increases. These findings suggest that including noise color of matrix elements in structured population projections may be important in many species, but
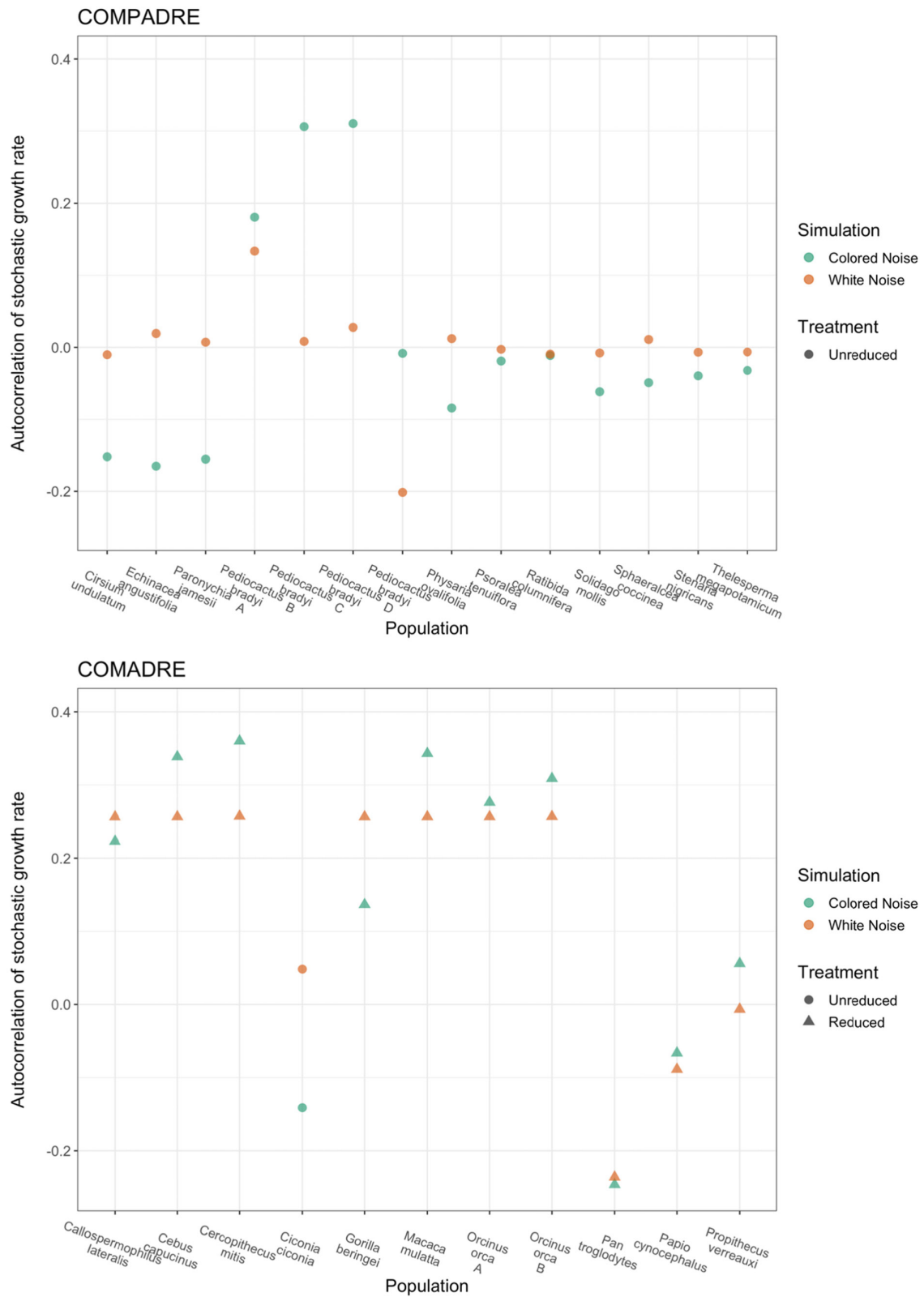
Figure 2. Temporal autocorrelation of the growth rate in population simulations including and ignoring the noise color of matrix elements. We ran 20 000 stochastic matrix population projections for each of 14 plant populations from COMPADRE and 11 animal populations from COMADRE. All populations with matrices larger than 3×3 had juvenile stage-classes pooled to reduce them to 3×3 (reduced). 10 000 simulations incorporated the observed temporal autocorrelation of the matrix transitions (colored noise), and 10 000 assumed no temporal autocorrelation in the matrices (white noise). We then averaged the temporal autocorrelation of the stochastic growth rate across each set of 10 000 projections.
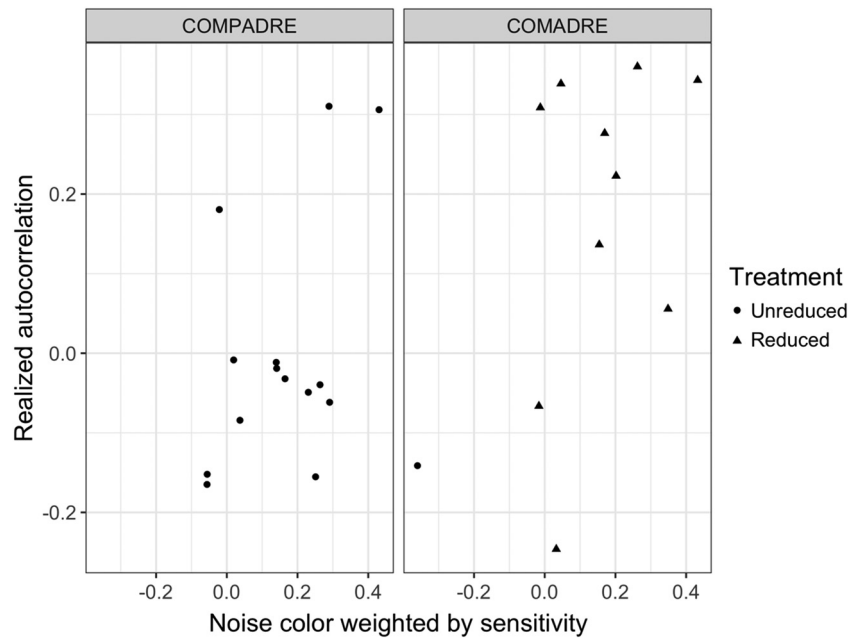
Figure 3. No relation between mean autocorrelation of the growth rate weighted by sensitivity of matrix elements and realized autocorrelation of the growth rate in simulations. A scatterplot of the realized autocorrelation of the stochastic growth rate averaged over 10 000 stochastic matrix population projections incorporating observed temporal autocorrelation of matrix transitions (y-axis) and the temporal autocorrelation averaged over the observed temporal autocorrelation of matrix transitions weighted by sensitivity of population growth rate to matrix elements (x-axis). All populations with matrices larger than 3×3 had juvenile stage-classes pooled to reduce them to 3×3 (reduced).

that effects of these inclusions can depend on how the population is structured in the model.

The processes that drive noise color of demographic rates can potentially be both extrinsic, e.g. effects of environmental variation (Paniw et al. 2018), and intrinsic, e.g. effects of among-individual synchrony in resource allocation (Miyazaki 2011). Observed patterns may also be affected by the numerical scale of vital rates. For example, the intrinsic boundedness of survival rates at 0 and 1 may cause spurious autocorrelations, in a similar way as has been shown for correlations of vital rate elasticity and variance (Morris and Doak 2004, Bjorkvoll et al. 2016). This may be especially true for populations with high survival in adult stage classes, such as the primates and orcas in our study, where survival frequently reaches the upper bound. However, in our simulations, boundedness produced a negative bias in temporal autocorrelation at very high and very low survival, which makes our findings of mostly positive temporal autocorrelation in the survival transitions of long-lived species all the more striking.

We suggest that some of the observed patterns have plausible biological explanations. For the plant populations, we found that fertility matrix elements exhibited bluer noise than survival elements. This would appear to match the pattern of annual variation often found in plants, where seed production tends to alternate between high and low reproductive modes on a supra-annual basis. The redder noise in survival might potentially have been driven by red noise in the variation of environmental factors, if survival is more

sensitive to environmental fluctuations than fecundity in these populations. In contrast to the plants, we found no similar pattern in noise color for the animal populations. It cannot be determined from our findings whether this is due to a general demographic difference between animals and plants, an artefact of the taxonomic bias toward primates in the animal matrices and towards short-lived species in the plant matrices, or indeed due to statistical artefacts. It is also possible that autocorrelations are affected by population-level processes like density dependence, which we would expect to cause cyclical temporal variation in fertility and survival when the population is near carrying capacity. More research will be required to determine what might drive these patterns, preferably further decomposing life cycles by investigating the vital rates that underlie matrix elements.

The stochastic growth rate of the populations had no relationship with the noise color of matrix elements weighted by stochastic sensitivity. This may suggest that matrix elements that do not strongly influence the magnitude of the population growth rate still influence its temporal autocorrelation. However, when predicting which matrix elements contribute most to the autocorrelation of the growth rate, alternate measures such as extensions of Tuljapurkar and Haridas's (2006) measure of the sensitivity of noise color of the population growth rate, that includes effects of changes in matrix elements, would be necessary.

We found a strong influence of stage structure on the noise color of the growth rate, which may explain the
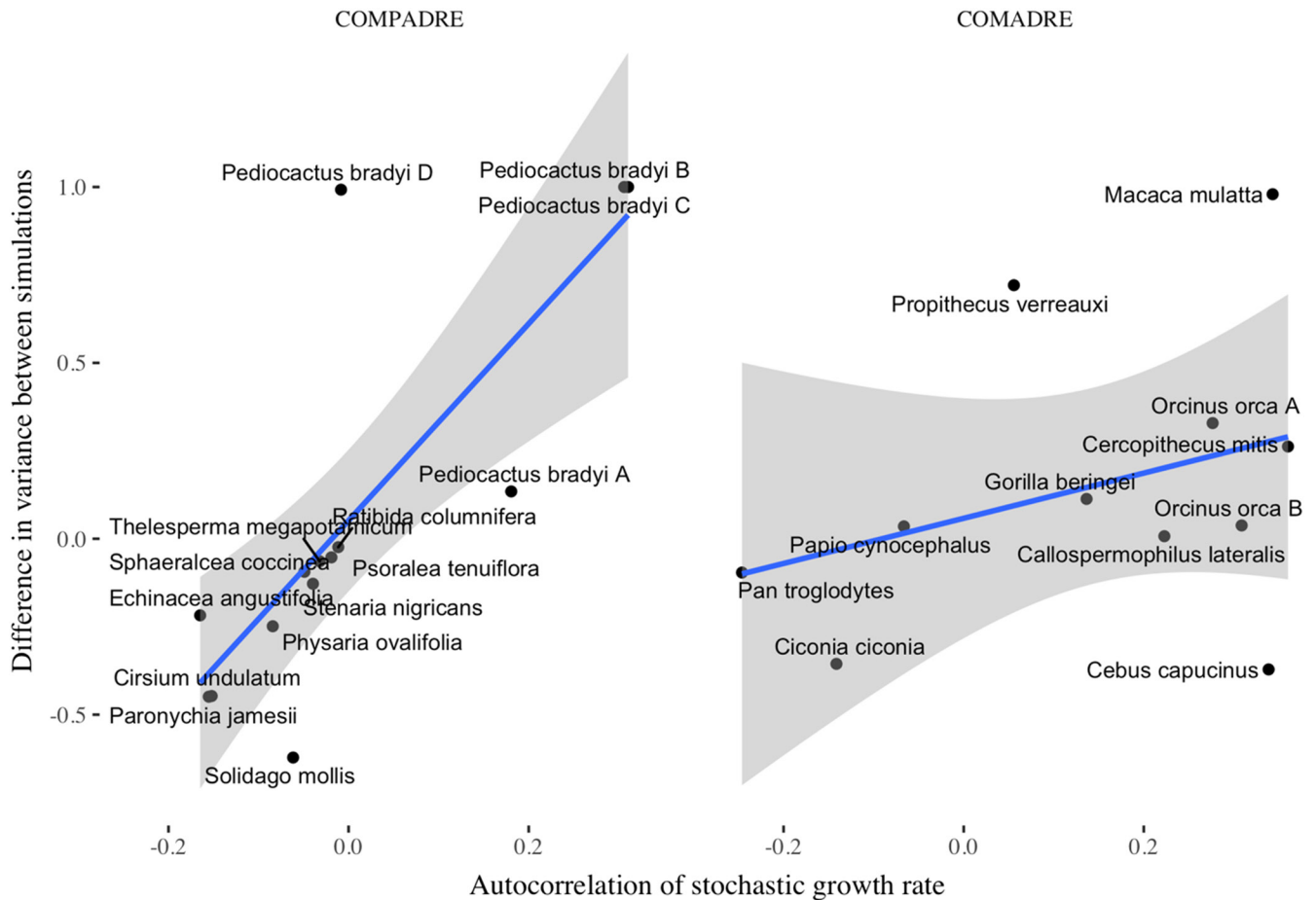
Figure 4. Variance in final population sizes in white noise and colored noise matrix model simulations. We ran 20 000 stochastic matrix population projections for each of 14 plant populations from COMPADRE and 11 animal populations from COMADRE. All populations with matrices larger than 3×3 had juvenile stage-classes pooled to reduce them to 3×3 (reduced). 10 000 simulations incorporated the observed temporal autocorrelation of the matrix transitions (colored noise), and 10 000 assumed no temporal autocorrelation in the matrices (white noise). The plant populations exhibit a direct relationship between the autocorrelation of the stochastic growth rate in the colored noise simulations (x-axis) and the relative difference in final population size variance between the colored and white noise simulations, where positive values indicate higher variance in population sizes in the colored noise simulations and negative values indicate higher variance in the white noise simulations (y-axis). In the animal populations there is no clear relationship between these variables.

deviations we found from the sensitivity to matrix elements. When we pooled the juvenile age-classes of animal populations with large matrices so the dimensionality was reduced to 3×3, the temporal autocorrelation of the growth rate decreased in both colored noise and white noise simulations. That the decrease was similar in both the colored and white noise simulations strongly suggests that a large component of noise color comes from the stage structure, since the white noise simulations had no other possible sources of temporal autocorrelation. This finding is consistent with previous studies that indicate decreasing matrix dimensionality affects the elasticities of matrix elements, increasing the importance of stasis and fecundity and decreasing the importance of growth (Enright et al. 1995, Salguero-Gomez and Plotkin 2010). Although correlations between vital rates are known to increase population fluctuations (Jongejans et al. 2010), when we omitted correlations between matrix elements,

there was little effect on the noise color of the growth rate. However, when we simplified the stage structure of larger matrices, the corresponding change in cross-correlations may have had a greater effect.

We found greater variance in population trajectories as temporal autocorrelation increased in our plant population simulations. Accordingly, extinction risk increased with red noise. This corroborates several previous findings in unstructured and structured population models with temporal autocorrelation (Heino and Sabadell 2003, van de Pol et al. 2011, Paniw et al. 2018). However, we did not observe this clear relationship in the animal data. It is likely that the species in our animal dataset may differ from each other in important ways that obscure any potential pattern. Indeed, these species range from long-lived primates to short-lived rodents and include both aquatic and terrestrial species. In contrast, most plants were short-lived and all were terrestrial. As more
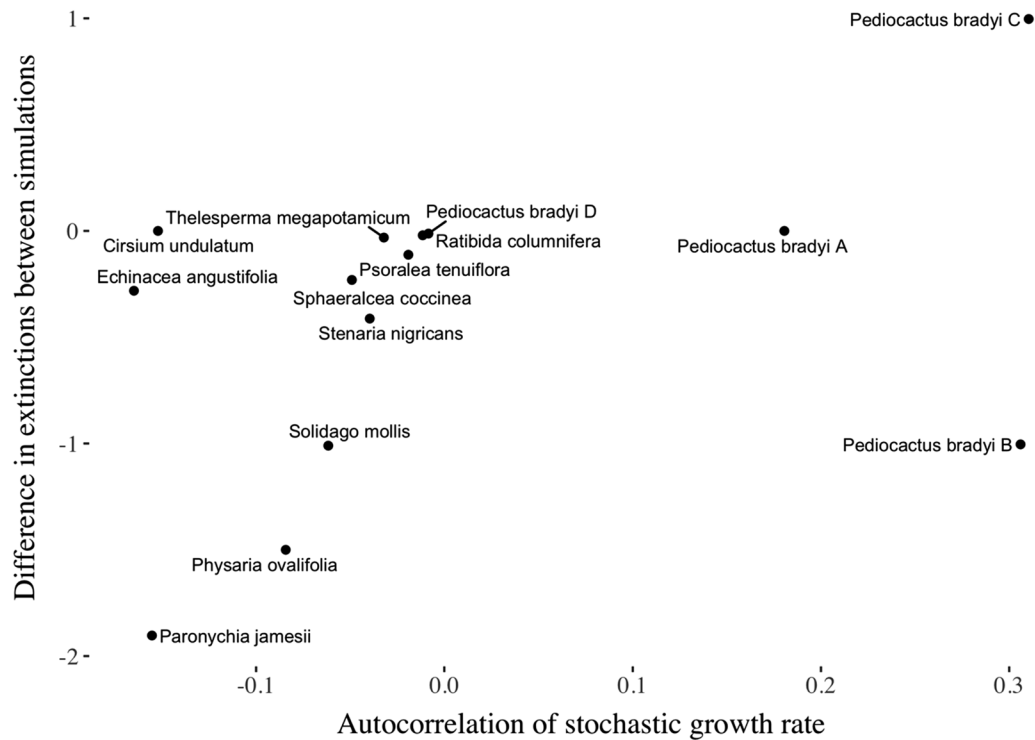
Figure 5. Relationship between temporal autocorrelation of the growth rate and relative extinction risk in colored and white noise population models. We ran 20 000 stochastic matrix population projections for each of 14 plant populations from COMPADRE, of which 10 000 incorporated the observed temporal autocorrelation of the matrix transitions (colored noise), and 10 000 assumed no temporal autocorrelation in the matrices (white noise). We observed a direct relationship between the autocorrelation of the stochastic growth rate in the colored noise simulations (x-axis) and the relative difference in extinctions between the colored and white noise simulations, where positive values indicate higher extinction risk in the colored noise simulations and negative values indicate higher extinction risk in the white noise simulations (y-axis).

long-term studies become available, perhaps clearer patterns can be found if comparing only species that are demographically similar, analogously to how, for example, covariation of life history traits across mammals changes when accounting for body size (Bielby et al. 2007).

In conclusion, we suggest that including the colored noise of matrix elements into population models can provide insight into the dynamics of structured populations. Our results show that temporal autocorrelation in demographic rates differs among species, among populations of the same species, and among life cycle stages in the same population. This suggests that detailed long-term demographic data is needed to advance ecological and evolutionary theory by incorporating effects of memory in time series. We present the colorednoise package in R as a tool for other researchers to investigate the temporal autocorrelation of demographic rates in their own long-term population time series.

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Supplementary material (available online as Appendix oik-06438 at <www.oikosjournal.org/appendix/oik-06438>). Appendix 1.