

Negative relationships between species richness and temporal variability are common but weak in natural systems

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Abstract. Effects of species diversity on population and community stability (or more precisely, the effects of species richness on temporal variability) have been studied for several decades, but there have been no large-scale tests in natural communities of predictions from theory. We used 91 data sets including plants, fish, small mammals, zooplankton, birds, and insects, to examine the relationship between species richness and temporal variability in populations and communities. Seventy-eight of 91 data sets showed a negative relationship between species richness and population variability; 46 of these relationships were statistically significant. Only five of the 13 positive richness–population variability relationships were statistically significant. Similarly, 51 of 91 data sets showed a negative relationship between species richness and community variability; of these, 26 were statistically significant. Seven of the 40 positive richness–community–variability relationships were statistically significant. We were able to test transferability (i.e., the predictive ability of models for sites that are spatially distinct from sites that were used to build the models) for 69 of 91 data sets; 35 and 31 data sets were transferable at the population and community levels, respectively. Only four were positive at the population level, and two at the community level. We conclude that there is compelling evidence of a negative relationship between species richness and temporal variability for about one-half of the ecological communities we examined. However, species richness explained relatively little of the variability in population or community abundances and resulted in small improvements in predictive ability.

Key words: communities; cross-validation; diversity; populations; predictive ability; species richness; stability; temporal variability.

INTRODUCTION

Over the last several decades, community ecologists have used theory (Elton 1958, May 1973, Doak et al. 1998), experiments (McGrady-Steed et al. 1997, Venail et al. 2015), and observational studies (Romanuk and Kolasa 2002, Steiner 2005) to address the question of whether diversity causes stability in ecological communities (McCann 2000) without reaching a clear conclusion. One source of confusion in the diversity–stability debate has been whether we were referring to community stability (i.e., fluctuations in the combined abundance of all species in a community) or population stability (i.e., fluctuations in the abundance of individual species). There is ubiquitous evidence of a negative relationship between species richness and temporal variability in *community* abundance (Tilman and Downing 1994, Cottingham et al. 2001) but the evidence of a

relationship between species richness and temporal variability in *population* abundance is less convincing. This paper examines the relationship between species richness (i.e., one index of diversity) and both population and community temporal variability in natural communities.

Population stability

There have been relatively few explicit theoretical examinations of the relationship between species richness and population temporal variability. Most of those examined multi-trophic level communities and indices of stability other than temporal variability. Early in the debate, MacArthur (1955) argued that population-level stability should be *greater* when species richness is high because there would be more sources of energy to offset species fluctuations.

In contrast, Robert May's (1973) models suggested that population stability should be *lower* when species richness is high. Other theoretical studies since then have reached similar conclusions (e.g., Haydon 1994). Tilman's (1999) models predicted that if (1) total community abundance is independent of species richness, (2) abundances are equally

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distributed among species, and (3) the slope of the log (mean)–log(variance) relationship is between 1 and 2 (as it usually is), then population variability should increase with species richness. Further, if there is strong overyielding, Tilman's models predict that population variability increases with species richness if that slope is between zero and two. However, Moore et al. (1993) suggested that the effect of species richness on population stability was more complex than some models suggested and the strength of the relationship depended on productivity.

Experimental results are more common but have also not been definitive. Field studies (in Minnesota [Tilman 1996] and in Mediterranean grasslands [Caldeira et al. 2005]) and laboratory experiments (McGrady-Steed and Morin 2000, Carr et al. 2002, Gonzalez and Descamps-Julien 2004) have found that increased diversity can result in greater population variability, lower population variability, or no relationship between diversity and population variability. Fewer studies have examined the relationship between diversity and population stability in natural communities, but these generally find a negative relationship between diversity and temporal variability (Cottingham et al. 2001).

While most research that has directly examined the relationship between species richness and population variability has assumed that diversity drives population variability, two related areas of ecological research, population persistence and coexistence theory, propose that population variability drives diversity. Theory suggests that population variability increases the risk of extinction (Pimm et al. 1988, Simberloff 1988, Lande 1993). Further, most empirical evidence also suggests that population variability and extinction risk are positively correlated (Karr 1982, Forney and Gilpin 1989, Oberdorff et al. 2001), although there are exceptions (Vucetich et al. 2000). In addition, modern coexistence theory (Chesson 2000) predicts that negative frequency dependence (i.e., high growth rates at low relative abundance) is one of two fundamental requirements for coexistence - the other is relatively small differences in long-term mean fitness among coexisting species (Adler et al. 2007, Vellend 2016). Negative frequency dependence is a form of density-dependent population regulation. It implies reduced population variability when population densities are low. Thus, for a given level of total community abundance, population variability should be lower when species richness is high. Thus, although coexistence theory rarely explicitly addresses the relationship between population variability and species richness, it does imply that, *all other things being equal*, there will be a negative relationship between species richness and population variability.

Community stability

Theoretical studies generally predict a negative relationship between species richness and community variability in temporal abundance, which is consistent with recent evidence that both species richness and community abundance are regulated in natural communities (Gotelli et al. 2017). This could occur because of (1) asynchronous responses of different species to the environment, (2) compensatory dynamics, and (3) overyielding (Loreau and de Mazencourt 2013). Higher stability in high species richness assemblages could also occur

for statistical reasons. If population variances are a power function of the mean population size (Taylor's Law), and if populations fluctuate through time independently, then the variation of total abundance will be greater in assemblages with a few abundant species than in assemblages with many, less abundant species (Doak et al. 1998).

Experimental results have been mixed. Most studies have shown a negative relationship between species richness and community variability (Tilman and Downing 1994, McGrady-Steed and Morin 2000, Caldeira et al. 2005) but not all (Petchey et al. 2002, Zhang and Zhang 2006). Research in natural communities has been less common but has generally shown a negative relationship between species richness and temporal variability (Romanuk and Kolasa 2004, Steiner 2005, Mikkelsen et al. 2011, Kuiters 2013), although there have been examples of a positive relationship (Kennedy et al. 2003). More recently, Hautier et al. (2014) showed that diversity was positively correlated with community stability in natural grasslands but that the effect was weakened by eutrophication. A recent meta-analysis has shown that there is no relationship between stability and diversity in natural food webs, but the evidence is still unclear for single trophic level communities (Jacquet et al. 2016). A second meta-analysis examining the effects of species richness on both community and population stability found that the effects of diversity on community stability were consistent and positive, while the effects on population stability were variable and dependent on the experimental design (Campbell et al. 2011).

The purpose of this study is to test the generality of the stability–diversity relationship among natural systems. We examined the empirical relationship between population variability, community variability, and species richness in 91 multiple-site, -year, and -species data sets. We assess the cross-validated predictive ability and transferability (Houlahan et al. 2017) of models to locations that were not used to build the models.

MATERIALS AND METHODS

Data sets

We compiled 91 multi-species, -time, -site data sets from 27 different regions across three continents (Fig. 1) to examine the relationship between mean species richness and temporal variability in population/community abundance (DataS1:DatasetDescription.csv). Seventy-five of the data sets are publicly available from Long-Term Ecological Research (LTER) data catalogs or from the Ecological Society of America (ESA) data archives. The remaining 16 sets were publicly available on the web, available upon request, or provided by the lead researchers responsible for a particular data set. The indices of abundance used in the 91 data sets were either number of individuals, areal cover, cover by percentage, or biomass. We edited each data set to resolve ambiguous taxa. The general rules for editing data sets were, (1) if individuals were designated as “unknown,” taxa were deleted; (2) records of individuals that were only identified to genus were treated as a species IF there were no records where individuals were identified to species in that genus; (3) if there were individuals that were only identified to genus



FIG. 1. Map of 27 regions where studies occurred.

AND there were also individuals identified to species for one or more species in that genus AND there were five or more records at only the genus level, then all individuals of that genus were merged and treated as a single species; and (4) if there were individuals that were only identified to genus AND there were also individuals identified to the species for one or more species in that genus AND there were fewer than five records of individuals at the genus-only taxon, then the records for the genus-only individuals were deleted. The rationale underlying this approach was that if there were many genus-only records (i.e., five or more) we were more comfortable collapsing all species of a genus to a single taxon than discarding the genus-only records. If there were few genus-only records (i.e., fewer than five) then we were more comfortable discarding those records and maintaining the distinctions among species.

The data sets used in the analysis included plants (71), mammals (8), birds (7), insects (3), and zooplankton (2). There were several data sets from the same geographic area because measurements were taken (1) at different spatial scales (e.g., plot and field scales for the E054 experiment at the Cedar Creek site), (2) in different seasons (fall and winter small mammal trapping at the Konza site), or (3) on different taxa (e.g., rodents and plants at the Portal site). Eighty-one of 91 data sets were from North America, so there were too few data sets from outside North America (DataS1: DatasetDescription.csv) to evaluate differences among continents.

Statistical analysis

Population.—We used two types of regression analyses to examine the relationship between population variability and species richness: (1) linear mixed models (LMM) and (2) site

variability indices (SVI and SV_2). In both, sites are the unit of replication for each data set.

1. Mixed model analysis (LMM).—The LMM models we used were (1) $\log(\sigma^2)_{ij} = c_0 + c_1 \log(\text{MSR})_{ij} + c_2 \log(\mu)_{ij}$ and (2) $\log(\text{MSR})_{ij} = c_0 + c_1 \log(\sigma^2)_{ij} + c_2 \log(\mu)_{ij}$. MSR_{ij} is the mean species richness associated with species i at site j , σ^2_{ij} is the variance in population abundance for species i at site j , μ_{ij} is the mean population abundance of species i at site j , and c_0 , c_1 , and c_2 are the fixed parameter estimates (i.e., intercept and slope coefficients). Note that we did not include the error term in equations simply to reduce the length of models. Because we were examining the effect of species richness on *population* variability, each species was assigned a species richness value (i.e., the species richness of the community in which they occur), which is analogous to what was described as “observed variability” in Campbell et al. (2011). The parameter estimates of interest in these analyses were the slope estimate for $\log(\text{MSR})$ in Model 1 and the slope estimate for $\log(\sigma^2)$ in Model 2. Models one and two are the same except that $\log(\text{MSR})$ and $\log(\sigma^2)$ switch positions between dependent and independent variable. We did this because the causal direction of the species-richness–temporal-variability relationship has not been clearly demonstrated. One reason to prefer Model 2 is that the independent variables of $\log(\text{MSR})$ and $\log(\mu)$ are unlikely to be as strongly correlated as $\log(\mu)$ and $\log(\sigma^2)$, the independent variables in Model 1. There are four versions of each model because we built models assuming (1) random intercept, (2) random intercept and random slope for $\log(\mu)_{ij}$, (3) random intercept and random slope for $\log(\text{MSR})_{ij}$ (or $\log(\sigma^2)_{ij}$), and (4) random intercept and random slope for both independent variables. The models were fit using

the nlme package in R with the default restricted maximum likelihood approach, and we reported the parameter estimates from the best model as determined by AIC scores. In 50 of 91 cases where $\log(\sigma^2)$ was the dependent variable, the best model assumed a random intercept and random slopes for both $\log(\mu)$ and $\log(\text{MSR})$ (Table 1). In 38 of 91 cases where $\log(\text{MSR})$ was the dependent variable, the best model assumed only a random intercept (Table 1). We included $\log(\mu)$ in these models because, ideally, any comparison of temporal variability among groups should be independent of mean abundance.

Other statistics have been used to estimate population variability independent of the mean (e.g., the coefficient of variation, the inverse of the coefficient of variation, or the standard deviation of the logarithms of abundances). However, McArdle et al. (1990) demonstrated that these are only mean-independent indices of variability when the slope of the $\log(\mu)$ – $\log(\sigma^2)$ relationship equals exactly two. Using mixed models that assume random intercepts across all species but a fixed slope for the $\log(\mu)$ – $\log(\sigma^2)$ and $\log(\mu)$ – $\log(\text{MSR})$ relationships, we found that the estimated slopes varied among the 91 data sets from 1.09 to 1.89, with a mean value of 1.53. We therefore preferred mixed models that include mean abundance as an independent variable, rather than models that attempt to standardize variance.

All models were fit separately for each of the 91 data sets. Mean effect size was estimated by calculating the mean slope across all data sets weighted by the inverse of the standard error of the slope estimate. We used the $R^2\text{glmm}$ package in R and the Nakagawa-Schielzeth method (Nakagawa and Schielzeth 2013) to calculate R^2 for mixed models.

2. Site variability indices (SVI_1 and SVI_2).—2.1. Site variability indices (SVI) calculations.— SVI_1 : The first step was to fit the linear mixed model $\log(\sigma^2)_{ij} = c_1 + c_2 \log(\mu)_{ij}$, where σ^2_{ij} is the variance in population abundance for species i at site j , μ_{ij} is the mean population abundance of species i at site j and c_1 and c_2 are the fixed intercept and slope estimates, respectively. This model allowed for a different $\log(\mu)$ – $\log(\sigma^2)$ relationship for each species and provided residuals (i.e., observed – predicted) for each species at each site in a data set. Thus, if a site had 50 species, there were 50 different residuals, one for each species. A positive residual for species i at site j implied that species i was more variable than would be expected for its mean abundance at site j

while a negative residual implied that it was less variable than would be expected for the observed mean abundance at site j . The second step was to calculate the mean residual across all species for each site to obtain an estimate of site-level variability,

$$SVI_j = 1/s \sum_{i=1}^s \text{Res}_{i,j}$$

where $\text{Res}_{i,j}$ = observed – predicted for species i at site j .

Thus, each site had a single number that represented its “average” variability, which is analogous to what was described as “mean variability” in Campbell et al. (2011). A large positive mean residual at site j implied that, on average, species were more variable than would be expected for their mean abundances at site j and a large negative residual implied that species were, on average, less variable than would be expected for their mean abundances at site j .

SVI_2 : Despite our reservations about using indices related to the coefficient of variation, we also analysed the data using the mean of temporal stability sensu Tilman (1996), or (μ_i/σ_i) (i.e., the inverse of the coefficient of variation), where μ_i is the mean abundance of species i over the census period and σ_i is the standard deviation of the abundance of species i over the census period, averaged across all species in a community. That is, $SVI_2 = 1/S \times \sum_{i=1}^S \mu_i/\sigma_i$ (S is the number of species in the community). We used this index because it will be more familiar to many readers. Here, a large positive value implies lower temporal variability. To avoid confusion, we emphasize that the two site variability indices run in opposite directions: large positive SVI_1 values imply high temporal site variability and large positive SVI_2 values imply low temporal site variability.

2.2. Mean species richness calculation (MSR).—The mean number of species across all years at a particular site is $MSR = \sum_{t=1}^T SR_t/T$, where SR_t is the number of species in year t , and T is the total number of years that the site was surveyed.

We then carried out four sets of simple regressions

$$SVI_{1,j} = c_1 + c_2 \log(\text{MSR}_j) + \varepsilon$$

$$\log(\text{MSR}_j) = c_1 + c_2 SVI_{1,j} + \varepsilon$$

$$SVI_{2,j} = c_1 + c_2 \log(\text{MSR}_j) + \varepsilon$$

$$\log(\text{MSR}_j) = c_1 + c_2 SVI_{2,j} + \varepsilon.$$

Therefore, for each of $SVI_{1,j}$ and $SVI_{2,j}$, there was a single SVI and MSR value for each site j in a particular data set. We ran simple linear regressions of the site variability index on $\log(\text{MSR}_j)$ for each of the 91 data sets.

Community.—We used multiple linear regression models to examine the relationship between species richness and temporal variability in total community abundance. Again, we used two approaches to estimate community variability.

1. CVI_1 .—As described above for populations, the coefficient of variation and other alternative measures are only

TABLE 1. Distribution of “best” models as selected by the Akaike information criterion (AIC) for population-level linear mixed model analyses.

Dependent variable	Model (random term)	Best model (no. data sets)
$\log(\text{variance})$	intercept only	3
$\log(\text{variance})$	intercept, $\log(\text{mean})$	50
$\log(\text{variance})$	intercept, $\log(\text{MSR})$	0
$\log(\text{variance})$	intercept, $\log(\text{mean})$, $\log(\text{MSR})$	38
$\log(\text{MSR})$	intercept only	38
$\log(\text{MSR})$	intercept, $\log(\text{mean})$	15
$\log(\text{MSR})$	intercept, $\log(\text{variance})$	7
$\log(\text{MSR})$	intercept, $\log(\text{mean})$, $\log(\text{MSR})$	31

mean-independent if the slope of the $\log(\mu)$ – $\log(\sigma^2)$ relationship equals two (McArdle et al. 1990). Because slopes were less than two (i.e., because the variance was unlikely to be independent of mean abundance) we included mean abundance (μ_{CA}) as a covariate in the statistical models: $\log \sigma_{CA}^2 = c_0 + c_1 \log(\text{MSR}) + c_2(\log \mu_{CA})$.

To assess the contribution of the portfolio effect to any observed relationship between community variability and species richness we also examined the relationship between the sum of variances and species richness. The variance of community abundance or biomass can be expressed as the sum of all the species variances plus all the pairwise species covariances. The portfolio effect asserts that increases in species richness will have an effect on the first term (i.e., sum of all the species variances; Doak et al. 1998). To assess the contribution of the portfolio effect to any observed relationship between community variability and species richness we examined the relationship between the sum of variances and species richness while controlling for community abundance. That is, $\log \sum_{i=1}^s \sigma_{ij}^2 = b_0 + b_1 \log(\text{MSR})_j + b_2 \log(\mu_{CA})_j$ where MSR_j is the mean number of species at site j , σ_{ij}^2 is the variance of species i at site j , and $(\mu_{CA})_j$ is the mean community abundance at site j . Here, the left side of the equation is the \log_{10} of the sum of the variances in population abundance across all species in the community. We also regressed the slope estimate of the community-variability–species-richness relationship on the slope of the sum-of-variances–species-richness relationship. This allowed us to assess whether the effect of species richness on the sum of variances (i.e., the portfolio effect) might be a key driver of the community-variability–species richness relationship.

2. CVI_2 .—We examined the temporal stability of communities using the inverse of the coefficient of variation, μ_N/σ_N , where μ_N is the mean abundance of the entire community over the census period and σ_N is the standard deviation of the abundance of the entire community. We fitted the model $\mu_N/\sigma_N = c_0 + c_1 \log(\text{MSR})$. It is not appropriate to include $\log(\mu)$ as an independent variable in this model because the mean is already incorporated into the dependent variable.

We estimated the relationship between species richness and mean-independent temporal variability of community abundance for all 91 data sets using these two different indices. We calculated the partial R^2 for $\log(\text{MSR})$ for each data set using the *rsq* package in R. Mean effect size was estimated by calculating the mean slope across all data sets weighted by the inverse of the standard error of the slope estimate.

Except where specified, we presented standardized slopes (i.e., unstandardized slope/standard error of slope estimate).

Cross-validation and transferability.—**1. Cross-validation.**—We cross-validated both population (SVI) and community (CVI) models using k -fold cross validation in the *caret* package in R. Cross-validation for mixed models has not been developed in *caret*. When possible, we used $k = 10$, but we reduced k when sample size would result in fewer than five test subsamples (i.e., when there were fewer than 50 sites). In those cases, we set k such that there would be a minimum of five test subsamples. For all models where species richness was used as an independent variable, we compared the cross-validated predictive ability of models including species

richness as an independent variable with models that did not include species richness. For all models where variability was the independent variable, we compared the cross-validated predictive ability of models including variability as a variable with those that did not.

2. Transferability.—To assess transferability, we separated the data based on spatial location using approximately 75% of the data in the training set and 25% in the test set. Sites were assigned to training and test sets such that a continuous line could be drawn on a map separating the two (Wenger and Olden 2012). For 22 data sets, sites did not have spatial coordinates. Those data sets were not used in the transferability analyses. Training and test sites were not necessarily far apart; rather they were simply not interspersed. We created two to four training/test sets for each of the 69 remaining data sets. We then used the models built on the training set to estimate the predictive accuracy of these models for sites in different locations. For example, we created four training/test sets for the North American Breeding Bird Survey data: (1) all routes west of longitude 81° W to predict all routes east of longitude 81° W, (2) all routes east of 108° W to predict all routes west of 108° W longitude, (3) all routes north of 37° N latitude to predict all routes south of 37° N latitude, and (4) all routes south of 45° N latitude to predict all routes north of 45° N latitude. For data sets that were sampled in a single transect rather than a grid, we could only construct two training/test sets. In those cases, we used plots from approximately the first 75% of the transect to predict plots from the last 25% and plots from the last 75% of the transect to predict plots from the first 25% of the transect. To estimate the predictive performance of models containing two independent variables such as $\log(\sigma_{CA}^2) = b_1 + b_2 \log(\text{MSR}) + b_3 \log(\mu)$ we compared the full model to the nested models (1) $\log(\sigma_{CA}^2) = c_0 + c_1 \log(\mu)$ and (2) $\log(\sigma_{CA}^2) = c_0$. For full models with a single independent variable, such as, $\text{SVI}_1 = c_0 + c_1 \log(\text{MSR})$, there is a single nested model $\text{SVI}_1 = c_0$ against which predictive performance is assessed. We compared the root mean square error (across all sites in the test set) among models to identify which model had the best predictive performance.

For consistency, we will refer to the relationship between temporal variability (measured as the variance in population abundance, variance in community abundance, SVI_1 , SVI_2 , CVI_1 , and CVI_2) and species richness rather than also including references to the stability–species-richness relationship. This decision still has the potential to result in confusion because the SVI_2 and CVI_2 indices run in opposite directions to the other four indices and so a positive relationship between temporal variability and species richness for $\text{SVI}_1/\text{CVI}_1$ would be consistent with a negative relationship between temporal variability and species richness for $\text{SVI}_2/\text{CVI}_2$.

RESULTS

Population

LMM approach.—Seventy-eight of the 91 data sets showed a negative relationship between species richness and variance in population abundance when $\log(\sigma^2)$ was used as the dependent variable. Among those negative relationships,

46 were statistically significant ($P \leq 0.05$), while only five of the 13 positive relationships were statistically significant (Fig. 2A). Though more than one-half of the data sets showed a significant effect of species richness, the mean proportion of variation (R^2) in $\log(\sigma^2)$ explained by species richness was 0.005 (DataS1: R2Output.csv). If we examine only the statistically significant results, the mean proportion of variance explained was 0.007. The mean weighted unstandardized slope was -0.113 (Appendix S1: Fig. S1A) suggesting that, on average, a 10% decrease in species richness would result in a 1.2% increase in population variability. When species richness was used as the dependent variable, 71 of 91 data sets showed a negative relationship between variance in population abundance and species richness. Of those negative relationships, 37 were statistically significant ($P \leq 0.05$), while only four of the 20 positive relationships were statistically significant (Fig. 2B). The mean proportion of variation in species richness explained by $\log(\sigma^2)$ was 0.012 for all 91 data sets (DataS1: R2Output.csv) and 0.023, if we examine only the statistically significant results. The mean weighted unstandardized slope was -0.018 (Appendix S1: Fig. S1B) suggesting, on average, a 10% increase in population variance would result in a 0.2% decrease in species richness.

Site variability approach.— Seventy-three of 91 data sets showed a negative relationship between SVI_1 and species richness, of which 36 were statistically significant ($P \leq 0.05$). Three of the 18 positive relationships were statistically significant (Fig. 3A). The mean weighted unstandardized slope was -0.372 (Appendix S1: Fig. S2A). This slope suggests that, on average, a 10% increase in population variance would result in a 4.0% decrease in species richness. The mean proportion of variation in site variability (SVI_1) explained by species richness was 0.126 for all 91 data sets (SI 1) and 0.209 if we examine only the statistically significant results (DataS1: R2Output.csv). When we used SVI_2 as our index of population-level variability, 61 of 91 data sets showed a negative relationship between temporal variability and species richness (i.e., positive relationships between SVI_2 and species richness) and 34 were statistically significant ($P \leq 0.05$). Seven of the 30 positive relationships were statistically significant (Fig. 3B). The mean weighted unstandardized slope was -0.097 (Appendix S1: Fig. S2B), suggesting that, on average, a 10% decrease in species richness would result in a 1.0% increase in population variability. The mean proportion of variation in site variability (SVI_2) explained by species richness was 0.072 for all 91 data sets (DataS1: R2Output.csv) and 0.142 if we examine only the statistically significant results.

Population cross validation and transferability.— The evidence for a negative relationship between species richness and temporal variability based on cross-validated and transferred predictions with SVI_1 and/or SVI_2 as the dependent variable was more equivocal. Models that included species richness as a predictor of variability made better cross-validated and transferred predictions than models without species richness as a predictor in 35 of 69 data sets (note: there were 22 data sets for which transferability could not be assessed). Thirty-four of those 35 data sets showed a

negative relationship between species richness and temporal variability while only one showed a positive relationship (Appendix S2: Table S1). For the data sets where species richness improved predictive performance, the improvement in accuracy was 6.2% for SVI_1 (DataS1: PredictionErrorOutput.csv).

Community

We only present detailed results for CVI_1 because CVI_1 was much superior to CVI_2 for cross-validated and transferred predictive ability.

CVI_1 .— Fifty-three of 91 data sets showed a negative relationship between temporal variability and species richness and 26 of those negative relationships were statistically significant ($P \leq 0.05$) while only seven of the 38 positive relationships were statistically significant (Fig. 4). The mean proportion of variation (R^2) in species richness explained by $\log(\sigma^2)$ was 0.125 for all 91 data sets (DataS1: R2Output.csv) and 0.209 if we examine only the statistically significant results. The mean weighted unstandardized slope of the $\log(\text{species richness})$ – $\log(\text{community variance})$ relationship was -0.356 . Our results suggest that, on average, a 10% decrease in species richness would result in a 3.8% increase in community variance. The mean weighted unstandardized slope of the $\log(\text{community variance})$ – $\log(\text{species richness})$ relationship was -0.066 (Appendix S1: Fig. S3) suggesting, on average, a 10% increase in community variance would result in a 0.7% decrease in species richness.

CVI_2 .— Sixty-five of 91 data sets showed a negative relationship between temporal variability and species richness and 35 of those negative relationships were statistically significant ($P \leq 0.05$) while only five of the 26 positive relationships were statistically significant.

Portfolio effect.— Seventy-five of 91 data sets showed a negative relationship between species richness and the sum of variances after controlling for community abundance and 42 of those relationships were statistically significant. We found 16 of 91 data sets showed a positive sum of variances–species richness relationship and only five of those were statistically significant (Appendix S3: Fig. S1). In addition, we found a strong relationship between the slope of the community–variability–species–richness relationship and the slope of the sum-of-variances–species–richness relationship ($R^2 = 0.73$; Appendix S3: Fig. S2).

Community cross validation and transferability

CVI_1 .— Models that included species richness as a predictor of variability made better cross-validated and transferred predictions than models without species richness as a predictor in 31 of 69 data sets. Twenty-six of the 31 data sets showed a negative relationship between species richness and temporal variability while five showed a positive relationship (Appendix S2: Table S2). For the 31 data sets where species richness improved predictive performance, the mean improvement in accuracy was 11.3% for CVI_1 (DataS1: PredictionErrorOutput.csv).

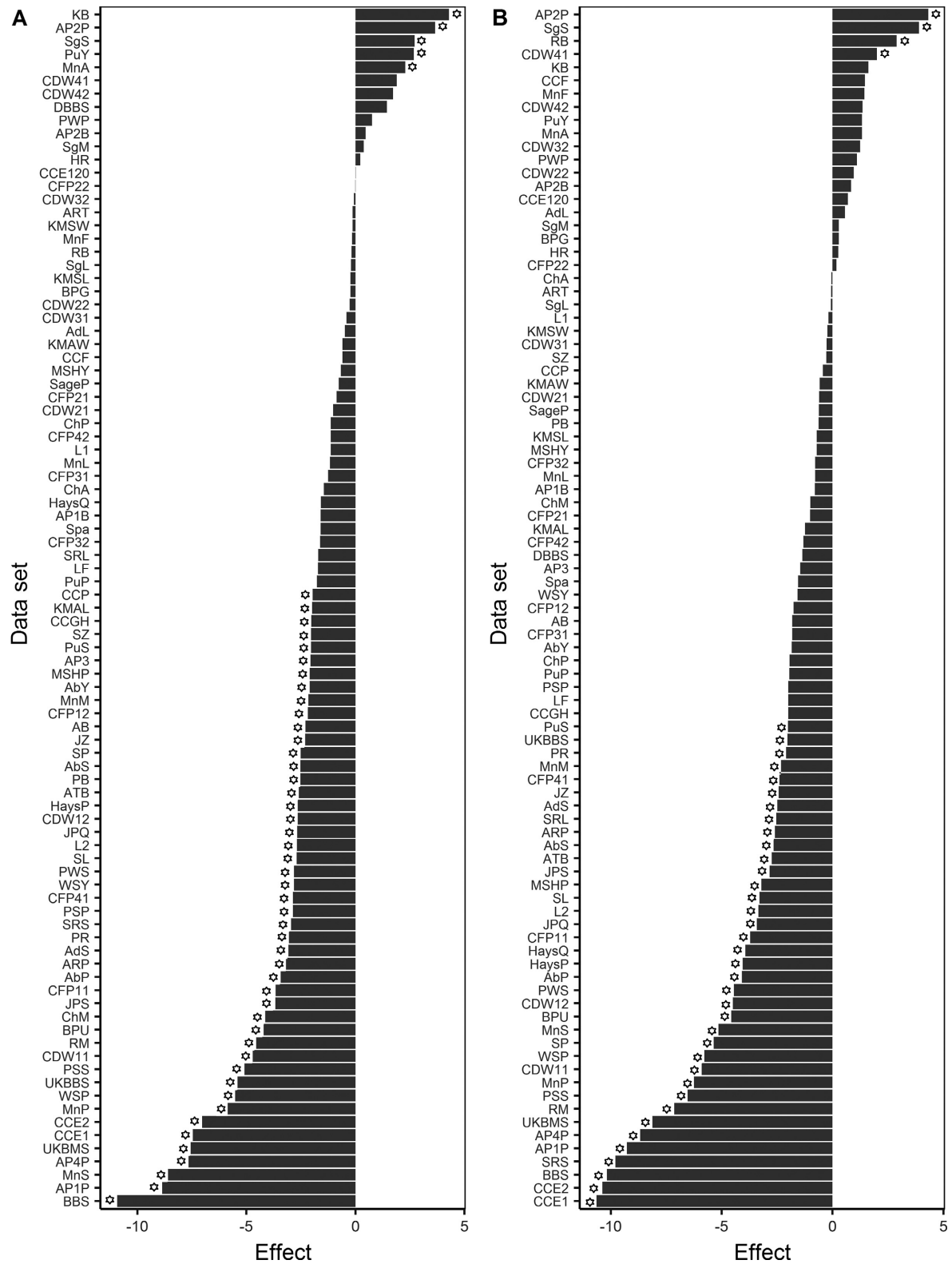


FIG. 2. (A) Histogram of the standardized population-level slope estimates for $\log(\text{MSR})_{ij}$ in the mixed model $\log(\sigma^2)_{ij} = a_1 + a_2 \log(\text{MSR})_{ij} + a_3 \log(\mu)_{ij}$ for each of the 91 data sets analysed. (B) Histogram of the standardized population-level slope estimates for $\log(\sigma^2)_{ij}$ in the mixed model $\log(\text{MSR})_{ij} = b_1 + b_2 \log(\sigma^2)_{ij} + b_3 \log(\mu)_{ij}$ for each of the 91 data sets analysed. MSR_{ij} is the mean species richness associated with species i at site j , σ^2_{ij} is the variance in population abundance for species i at site j , and μ_{ij} is the mean population abundance of species i at site j . Asterisks denote statistical significance ($P \leq 0.05$). See DataS1:DatasetDescription.csv for full name of abbreviated data set names.

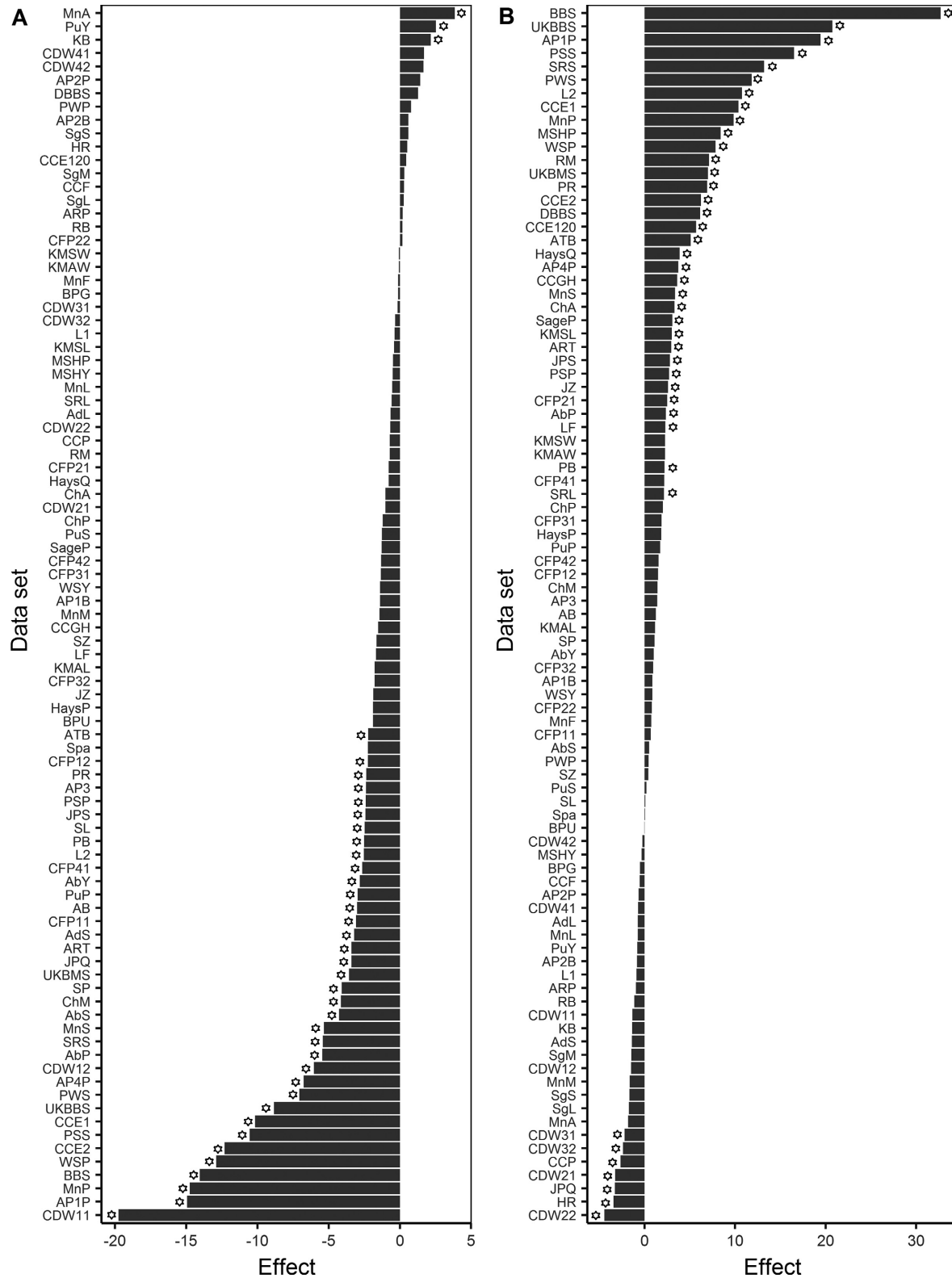


FIG. 3. (A) Histogram of the standardized population-level slope estimates for $\log(\text{MSR})$ in the simple linear regression model $\text{SVI}_{1,j} = a + \log(\text{MSR})_j$ for each of the 91 data sets analyzed. (B) Histogram of the standardized population-level slope estimates for $\log(\text{MSR})$ in the simple linear regression model $\text{SVI}_{2,j} = a + \log(\text{MSR})_j$ for each of the 91 data sets analysed. $\text{SVI}_{1,j}$ is a community-level measure of variability at site j based on the residuals from a regression relating the variance in population abundance to the mean abundance at site j . MSR_j represents the mean species richness. Asterisks denotes statistical significance ($P \leq 0.05$). See DataS1:DatasetDescription.csv for full name of abbreviated data set names.

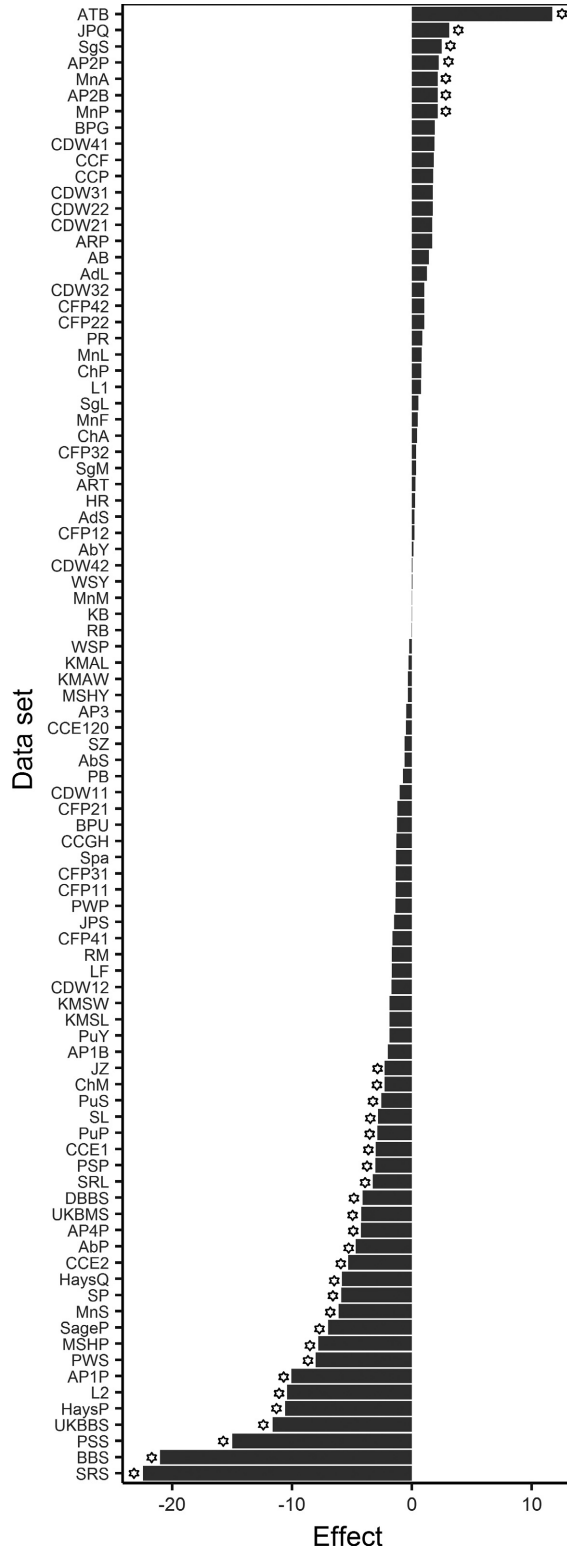


FIG. 4. Histogram of the standardized community-level slope estimates for $\log(\text{MSR})$ in the multiple regression model $\log(\sigma_{CA}^2)_j = c_0 + c_1 \log(\text{MSR})_j + c_2 \log(\mu)_j$ for each of the 91 data sets analysed. Asterisks denotes statistical significance ($P \leq 0.05$). $(\sigma_{CA}^2)_j$ is the variance in community abundance, MSR_j is the mean species richness at site j and μ_j is the mean abundance at site j , c_{0-2} are the fixed parameter estimates for the multiple regression model. See DataS1:DatasetDescription.csv for full name of abbreviated data set names.

Comparison of population and community relationships

There is a positive relationship between population- and community-standardized slopes, suggesting that the relationship between temporal variability and species richness at the population level does scale up to the community level (Fig. 5). However, the strength of this relationship was moderate ($R^2 = 0.23$).

Sample size and standardized effect

There was wide variability among data sets in the number of communities (i.e., sample size) that were available to examine relationships between temporal variability and species richness. The accuracy and precision of slope estimates were driven, in part, by sample size. We found a statistically significant negative relationship between log-transformed sample size and the standardized slopes of relationships between temporal variability and species richness. This suggests that, as more data were available to estimate slopes, the slopes were found to be increasingly negative (Appendix S4: Figs. S1A, S1B).

DISCUSSION

Key findings

Relationships between temporal variability and species richness are common in nature for both populations and communities. Where there was compelling evidence of a relationship between species richness and temporal variability, the relationship was usually negative. Further, the proportion of negative relationships is greater at the population than the community level. However, at both population and community levels, only about one-half of the data sets show significant, cross-validated, transferable relationships, and

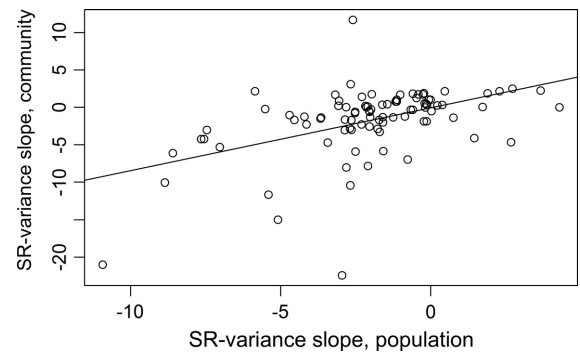


FIG. 5. Scatterplot of the relationship between standardized population-level slope estimates for $\log(\text{MSR})_{ij}$ in the mixed model $\log(\sigma_{ij}^2) = c_0 + c_1 \log(\text{MSR})_{ij} + c_2 \log(\mu)_{ij}$ and $\log(\text{MSR})_{ij} = c_0 + c_1 \log(\sigma_{ij}^2) + c_2 \log(\mu)_{ij}$ and standardized community-level slope estimates for $\log(\text{MSR})$ in the multiple regression model $\log(\sigma_{CA}^2)_j = c_0 + c_1 \log(\text{MSR})_j + c_2 \log(\mu)_j$ for each of the 91 data sets analysed. MSR_{ij} is the mean species richness associated with species i at site j , σ_{ij}^2 is the variance in population abundance for species i at site j , μ_{ij} is the mean population abundance of species i at site j , $(\sigma_{CA}^2)_j$ is the variance in community abundance, MSR_j is the mean species richness at site j and μ_j is the mean abundance at site j , c_{0-2} are the fixed parameter estimates for both the mixed and multiple regression models.

the even those relationships were generally weak. Further, including species richness in models improved the predictive ability by 6–15%.

Population stability and species richness

Our results suggest that, in general, the relationship between species richness and population temporal variability is negative. This result is consistent with many of the studies in natural systems in the literature. For example, Dovciak and Halpern (2010) found that there was a negative relationship between diversity and temporal variability in plant communities, although the relationship was impacted by plant type and successional stage; Mikkelsen et al. (2011) found that species richness and population temporal variability were negatively correlated in North American bird communities; Zhang et al. (2016) found a negative relationship between diversity and temporal variability in temperate grasslands even after controlling for nutrient additions; Yang et al. (2012) found a negative relationship between diversity and population temporal variability in a different set of temperate grasslands regardless of mowing or nutrient treatments; Proulx et al. (2010) showed a negative relationship between diversity and population temporal variability in experimental grassland systems; and Downing et al. (2014) found that population temporal variability decreased with species richness in zooplankton communities.

Species coexistence mechanisms have been a perennial topic of interest in ecology. Many studies have focused on negative frequency dependence that may result from factors such as the storage effect (Chesson 2000), density-dependent predation rates (Janzen 1970, Bagchi et al. 2014, Comita et al. 2014), and intraspecific vs. interspecific effects of competition (Yenni et al. 2012). Negative frequency dependence is expected to both reduce population variability and result in increased species richness (especially in systems where dispersal is unlikely to be a key driver of species richness; Velend 2016). Several recent studies have demonstrated a relationship between negative frequency dependence and species richness (LaManna et al. 2017, Yenni et al. 2017), which is additional indirect evidence of a negative relationship between diversity and temporal variability. In contrast, van Ruijven and Berendse (2007) found that, in general, population variability increased with species richness in experimental plant communities. Roscher et al. (2011) found a positive relationship between species richness and population temporal variability in experimental grasslands. Gonzalez and Descamps-Julien (2004) found population temporal variability increased with algal species richness. Thus, while more studies seem to show negative effects of species richness on population temporal variability, results are mixed. Indeed, several studies suggested that the relationship between diversity and population temporal variability depended on the species in the communities (Hector et al. 2010, Gustafsson and Bostrom 2011, Kuiters 2013).

Community and population ecology have approached the diversity–stability question from dramatically different perspectives. Ecological theory addressing population dynamics consistently shows that higher population variability increases the risk of extinction (Pimm et al. 1988, Simberloff 1988, Lande 1993) even in contexts where the observed

dynamics are unusual (Sinha and Parthasarathy 1996). In fact, population variability is so widely accepted as being positively associated with extinction that it is an explicit criterion for deciding which category of extinction risk will be assigned to a species in IUCN evaluations (Mace and Lande 1991). A logical corollary of a positive relationship between population variability and extinction risk is that species richness and population variability will be negatively correlated.

However, the usual interpretation of a negative relationship between diversity and population temporal variability in community ecology is that diversity confers population stability. Of the studies mentioned above, almost all implied or stated explicitly that the causal direction was from diversity to population stability. Only Dovciak and Halpern (2010) explicitly discussed the possibility that population temporal variability caused reduced diversity.

This bias is particularly puzzling because, although modern coexistence theory implies a negative relationship between population variability and species richness (Janzen 1970, Chesson 2000, Adler et al. 2007), several theoretical studies (May 1973, Haydon 1994, Ives et al. 1999, Tilman 1999) suggest a positive relationship between temporal variability and species richness, not the negative relationship observed more commonly in these data sets. There has been some experimental work that directly addressed the question by manipulating species richness and in most cases showed a positive relationship between temporal variability and species richness, but the manipulation was often indirect, (e.g., by enriching the food supply or increasing the ecosystem size) and so often did not provide conclusive evidence as to the causal direction.

Community stability and species richness

Negative relationships between species richness and temporal variability are less common for communities than for populations based on simple counts of the sign of the regression slope in our analyses. However, the more rigorous criterion of transferability would suggest that communities and populations are similar. There has been a great deal of theoretical discussion about what the expected relationship should be between diversity and stability (MacArthur 1955, Elton 1958, May 1973, Tilman 1999), but it has recently been suggested that empirical results, both experimental and, to a lesser extent, observational, have shown positive, negative, and neutral relationships (McCann 2000). However, there are many more examples of a negative relationship between community variability and diversity for both natural and experimental systems than positive relationships (Campbell et al. 2011). The preponderance of negative relationships is somewhat unexpected, given that there is compelling recent evidence that both species richness and community abundance are regulated in natural communities (Gotelli et al. 2017).

There has been disagreement about the likely mechanism for a general positive relationship between diversity and community temporal variability. The dominant explanations, the portfolio effect and the compensatory effect are fundamentally different. The portfolio effect predicts a negative diversity–variability relationship due to statistical averaging. Our analyses of the effects of species richness on the

sum of variances in natural communities suggest that the portfolio effect is making a significant contribution to the observed relationship between community variability and species richness. Some ecologists interpret evidence of the portfolio effect to mean that the negative relationship between community variability and species richness is a statistical inevitability. However, the portfolio effect relies on the assumption that, as species richness increases, community abundance stays constant and this combination seems to imply some kind of biological constraint. The most obvious one is interspecific competition. Thus, we should not interpret the portfolio effect, exclusively, as a statistical artefact but rather, another plausible mechanism responsible for observed diversity–stability relationships.

The compensatory effect requires that negative correlations among species increase in number and/or strength with diversity. Causes of negative correlations include interspecific competition and differing responses to environmental conditions but, regardless of mechanism, the effect must increase with species richness if species richness is to stabilize community abundance. In addition, overyielding is another proposed mechanism because if community abundance increases with species richness and the mean–variance scaling relationship is such that the slope of the $\log(\mu)$ – $\log(\sigma^2)$ relationship for community abundance is <2 then there will be a negative relationship between species richness and community variability. Most studies that found a negative relationship between community variability and diversity also found that statistical averaging played an important role (Li and Stevens 2010, Thibault and Connolly 2013, Downing et al. 2014, Zhang et al. 2016). Many of these studies found that species asynchrony increased with species richness (Hector et al. 2010, Li and Stevens 2010, Roscher et al. 2011, Thibault and Connolly 2013, Downing et al. 2014, Hautier et al. 2014, Zhang et al. 2016) and that overyielding played a role (Valone and Hoffman 2003, Jiang and Pu 2009, Hector et al. 2010, Mikkelsen et al. 2011, Loreau and de Mazencourt 2013). It has also been suggested that interspecific competition would be greater in more species-rich communities, but the intuitive idea that interspecific competitive interactions will stabilize community-level fluctuations may not be true. Ives et al. (1999) found that, under the most realistic conditions, interspecific competition resulted in greater community variability because decreases in covariance were more than offset by increased population variability.

Ecologists have not made much progress in distinguishing among the variety of explanations for diversity–stability relationships and there needs to be renewed investigation to identify the most important drivers of richness–stability relationships and how the relative importance of specific drivers changes with context.

Community vs. population effects

One early review of diversity–stability relationships showed that all studies demonstrated either a negative relationship between diversity and community variability or no clear relationship, while the few population-level studies showed a positive relationship between species richness and population variability or no relationship (Cottingham et al.

2001). More recently, the majority of studies have shown a negative relationship between community variability and species richness while the evidence is not as clear for a negative relationship between population variability and species richness (Yang et al. 2012, Vogt et al. 2013, Hautier et al. 2014, Rakowski and Cardinale 2016, Zhang et al. 2016). However, our results show that a larger proportion of the 91 data sets showed a negative relationship between population variability and species richness than community variability and species richness.

In addition, the relationship between sample size and the slope of the population temporal-variability–species-richness relationship was slightly stronger (as measured by R^2) and steeper than for community variability and species richness. So, despite the theoretical and empirical support in the literature being less definitive for a population diversity–stability relationship than for a community relationship, our results suggest that negative population species richness variability relationships are at least as common and as strong as community relationships.

Transferability

One of the strengths of this paper is that we have used spatial transferability as a more rigorous test of the relationship between temporal variability and species richness. We argue that this comparison is important because, if ecological models are not temporally or spatially transferable, it implies that they provide no understanding of the world beyond the time and place where the data were gathered. Here, the training set sites and test set sites were spatially separate but in relatively close proximity. It is reasonable to describe this test of spatial transferability as the “least” we would expect of ecological models.

CONCLUSIONS

- 1) About one-half of the data sets show statistically significant, cross-validated, spatially transferable relationships between species richness and temporal variability.
- 2) The mean proportion of variation in $\log(\sigma^2)$ explained by species richness was very small.
- 3) The large majority of these relationships between species richness and temporal variability are negative.
- 4) Including temporal variability as a predictor of species richness results in moderate increases in predictive ability.
- 5) There are systems where temporal variability and species richness are linked but many where they are not. We currently have no explanations for this difference among ecosystems.
- 6) The causal direction of diversity–stability relationships and the mechanisms driving these relationships in nature have not been identified and require additional investigation.

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