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Multiple links between species diversity and temporal stability in bird communities across North America

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ABSTRACT

Background: In experimental systems, the temporal stability of entire ecological communities usually increases with the number of species (called 'species richness'). In contrast, ecology has not discovered the pattern of stability with the complement of richness, which is evenness of species abundances. The job has been more difficult because many measures of species diversity combine richness with evenness.

Questions: Does the correlation of richness with stability occur in natural systems? What is the relationship of evenness to stability? Does diversity increase or decrease the stability of individual species populations? What mechanisms explain the relationships, if any, between diversity and stability?

Data: The 1966–2009 results of 1676 North American Breeding Bird (BBS) survey routes across the USA and Canada. Altogether, 617 bird species were registered with an average of 105 species observed per route. Climate variables were taken from the US National Oceanic and Atmospheric Administration, and Climate Services Canada databases.

Analytical methods: Disentangle richness from evenness and study their separate effects on stability. Perform statistical analysis of biological variables developed from the BBS data. Control for biological and climatic influences.

Results: Both the number of bird species and the evenness of their distributions positively affect the stability of entire bird communities. But richness and evenness do so through a contrasting set of mechanisms. Also, richness and evenness both positively affect the stability of individual populations. The link between evenness and mean population stability can be partly, but not completely, explained in terms of a previously established relationship between the mean and variance of abundance known as Taylor's Law.

Keywords: biodiversity, community stability, covariance effect, diminishing returns, over-yielding, population stability, portfolio effect, species evenness, species interactions, species richness, Taylor's Law, temporal stability.

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INTRODUCTION

The ongoing siege of biodiversity by human economic activity has prompted a growing number of laboratory and field experiments exploring the consequences for various aspects of ecosystem function, especially ecological stability (Ives and Carpenter, 2007). These experiments have helped researchers tease out the effects of biological diversity from other influences on stability. However, laboratory microcosms and field plots are very small compared with most of the real-world communities they are supposed to model (Pimm, 1991). Furthermore, controlled experiments always run the risk of introducing unrealistic factors into the system under study. It is always essential to test experimental results against observations of natural communities (Diamond, 1986).

In this study, we examined whether species diversity is linked to temporal stability among 1676 natural communities of birds across North America. While most experiments have focused solely on the number of species (richness), we also explored the evenness of species abundances, that is, how evenly distributed the number of individuals is among those species. Evenness is potentially important because if particular species become rare enough, they may cease to play significant roles in their ecosystems long before going extinct (Chapin *et al.*, 2000). Furthermore, experimental evidence suggests that while richness improves the stability of ecological communities, evenness may not (Ives and Carpenter, 2007; Isbell *et al.*, 2009).

We focus on temporal stability – the mean of a variable (in this case abundance) divided by its standard deviation – because it is empirically straightforward to estimate, can be applied to both individual populations and entire communities, and has recently been the subject of important discoveries (Mikkelson, 2009). As noted above, species richness has generally increased the temporal stability of experimental communities. But it has had inconsistent effects on experimental populations (Romanuk *et al.*, 2006; Tilman *et al.*, 2006). We therefore measured stability at both the community and the population level.

Lehman and Tilman (2000) enumerate three mechanisms by which species richness stabilizes communities: over-yielding, the portfolio effect, and negative covariance between species. To determine which, if any, of these mechanisms may be operating among North American birds, we parsed community stability into three mathematical components: the mean, over time, of the total number of birds irrespective of species (μ_C); the sum, over all species in the community, of the temporal variance of the number of birds in a given species ($\Sigma\mathrm{Var}_P$); and the sum, over all pairs of species, of the temporal covariance in their abundances ($\Sigma\mathrm{Cov}_P$). These three quantities relate to community stability (S_C) as follows:

$$S_C = \mu_C/(\Sigma\mathrm{Var}_P + \Sigma\mathrm{Cov}_P)^{1/2}.$$

Over-yielding would involve an increase in mean community abundance (μ_C) with richness and/or evenness. The portfolio effect would entail a decrease in the sum of the variances of individual species abundances ($\Sigma\mathrm{Var}_P$). And the covariance effect would entail a reduction in the sum of the covariances between species ($\Sigma\mathrm{Cov}_P$).

Previous work also offers a basis on which to predict a positive effect of species evenness on population stability. Taylor's Law is a well-confirmed relationship between the temporal mean and variance of abundance in single-species populations (see, for example, Taylor and Woiwod, 1980; Kilpatrick and Ives, 2003). Taylor's Law states that $\mathrm{Var}_P = c(\mu_P)^z$, with the exponent z usually lying between 1.0 and 2.0. Re-arranging Taylor's Law yields the following relationship between the mean abundance and stability of a population:

$$S_P = \mu_P/\sigma_P = (c)^{-1/2}(\mu_P)^{1-z/2}.$$

Here, population stability (S_P) is defined as discussed above (the temporal mean of abundance divided by its temporal standard deviation), and σ_P denotes that standard deviation (i.e. the square root of the variance). Since z is between 1.0 and 2.0, the exponent of this latter equation ($1 - z/2$) is between 0.0 and 0.5. Thus population stability increases with mean abundance, but with strongly diminishing returns. Because of the property of diminishing returns, going from a small mean population to a moderate mean population confers a much larger increase in stability than would the same size increase in mean population but from moderate size to large size.

Note that relatively even communities (by definition) have more moderately abundant species and fewer very rare or very common species, than do relatively uneven communities. Going from such an even community to an uneven one entails replacing some moderately abundant species with rare ones and some other moderately abundant species with common ones. Reducing a species abundance to rarity greatly diminishes its stability, but increasing it to commonness adds little to its stability. So the net effect of replacing an even community with an uneven one is a loss of average population stability. And a more even distribution of abundance among species should tend to result in greater average population stability.

Our data are taken from the North American Breeding Bird Survey (BBS), one of the most comprehensive biodiversity data sets in the world (Sauer *et al.*, 2008). Since 1966, qualified bird watchers have annually censused several thousand 25-mile routes throughout Canada and the USA (and now Mexico as well). We included only the survey runs deemed to be of high quality by BBS scientists, and we statistically controlled for average temperature and precipitation, as well as the variabilities of these key environmental variables. To help correct for the fact that estimates of physical and biological variability tend to increase with the time span covered (cf. Pimm and Redfearn, 1988), we included only routes with at least 10 years of high-quality surveys, initiated no later than 1975 and ending no earlier than 2000. These 1676 routes collectively range across 59 US states and Canadian provinces, and involve 617 species of bird.

METHODS

BBS volunteers record the number of birds of each species, every half mile along a given 25-mile route, once per year during the breeding season. The basic starting point for our analyses is the total number of individuals in a given species, observed in a given year across an entire route. We obtained our raw data from ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles, and performed our statistical analyses using R, version 2.12.1. Before analysing the data, we removed all runs (years) within each route that were deemed poor quality by BBS researchers.

For each route, we calculated the mean across years of its species richness (number of species) and evenness (the reciprocal of Simpson's dominance index, divided by richness). We chose the latter measure of evenness because it is commonly used and, unlike Shannon-Wiener evenness (Shannon-Wiener diversity divided by the logarithm of richness), Simpson evenness does not confound evenness with richness (Smith and Wilson, 1996). In addition to richness and evenness, we computed the temporal mean and stability of each route's total community abundance. For each species population within each route, we calculated the temporal mean, variance, and stability of its abundance. We then took the mean of population stability and the sum of population variance, and calculated the sum of population covariance over all species within a given route.

We statistically controlled for the mean and year-to-year standard deviations of two of the most important environmental variables – temperature and total annual precipitation – as well as latitude, longitude, key temporal variables, and body size as described below. The environmental statistics come from 1494 weather stations across Canada and the USA. We used ArcWeb 9.3.1 to identify which climatological stations are closest to which BBS routes. By special request, Climate Services supplied the stats for Canadian stations over the years 1971–2000. For US stations, we derived them for that same time span using raw data obtained at ftp://ftp.ncdc.noaa.gov/pub/data/ushcn/v2/monthly. Measures of variability tend to increase with the number of observations and with the length of time over which they are taken (Pimm and Redfearn, 1988). For this reason, we excluded from our analyses any routes that were surveyed for fewer than 10 years, which started later than 1975 or ended earlier than 2000. Even for routes thus surveyed in at least 10 years and spanning at least 1975–2000, we statistically controlled for the starting year, ending year, and total number of years surveyed. Finally, we controlled for body size, which has many important ecological consequences (Peters, 1983). Pimm (1991) found that vertebrate population stabilities tend to increase with mass up to 100 g, but then decrease with it past that threshold. We therefore added mean body mass, and the square of it, to the spatiotemporal and environmental controls described above. To compute the mean body mass for a given community, we took the abundance-weighted average, over all single-species populations within the community, of the mean body masses of those species.

Two final checks on the robustness of our results involve 'de-trending' and 'de-zeroing'. We de-trended the abundance data by regressing them on the years in which they were gathered, and then repeated our analyses using the temporal standard deviation of the residuals rather than that of the raw abundances. We did this for each population in each route, as well as for each route as a whole. De-trending helps correct for the possibility that any given population or community may have experienced a genuine temporal trend in total abundance over the past four to five decades, or for the possibility that different researchers may have done the observations in different years along the same route. Another potential issue with our population-level data set is that almost half the records are years in which a given species was not observed, despite being observed in at least one other year along the same route. Because each route is surveyed for only one day of a given year, absence of evidence for a given species' occurrence along a given route in that year does not provide compelling evidence of its true absence. Zeroes thus potentially lead to over-estimates of year-to-year variability in abundance. Therefore, we repeated our analyses of relationships between diversity and mean population stability after excluding all zeroes. Since some zeroes signify real absence, such exclusion could lead to underestimates of variability. Performing our analyses with zeroes included and excluded thus arguably brackets the true temporal variation experienced by these populations.

Since most of the statistics described above – as well as common mathematical transformations of them – are not normally distributed (Shapiro-Wilk P-values $\ll 0.05$), we relied on a non-parametric rank correlation coefficient, Kendall's τ, to test for associations among them. We made an exception by performing an ordinary least-squares regression of the logarithm of population stability on the log of population abundance. The reason for this exception is that for present purposes the parameter values – not just the direction and strength – of this latter relationship matter. (See the consideration of Taylor's Law given in the Introduction above and the Discussion below.) When controlling for the potentially confounding variables described above, we regressed a given dependent variable (e.g. community stability) on them, and then performed Kendall's non-parametric test of association between the residuals and a given independent variable of interest (e.g. species richness).

As with any study of natural systems, some unmeasured variable might account for the correlations observed between measured variables. Such variables might include life-history traits or the positions of populations within species' ranges. But by controlling for the spatial, temporal, and environmental variables described above, as well as body size, we hope to have addressed the most likely of such variables.

RESULTS

Species richness and evenness both have highly significant positive correlations with the temporal stability of North American bird communities (Figs. 1 and 2). Furthermore, species richness correlates significantly and positively with community stability, even after controlling for evenness; and likewise evenness after controlling for richness. These diversity–stability relationships also remain significant and positive after controlling for spatial, temporal, and environmental variables – including environmental variability – and body size (Table 1). Finally, they hold for both raw and de-trended community stability (see Methods).

While richness and evenness both correlate positively with community stability, these two aspects of species diversity have contrasting relationships with the determinants of community stability. Richness relates positively to the temporal mean of community abundance, and the summed covariances of population abundance, but negatively to the summed variances of population abundance. In contrast, evenness relates negatively to all three determinants of community stability (see Table 2).

Species diversity relates significantly and positively not only to community stability, but also to mean population stability (Figs. 3 and 4). Except for one analysis, this is true after applying the same statistical controls as those reported above for community stability (Table 3). The exception occurs when all spatiotemporal and environmental variables, body size, the square of body size, and species richness – twelve variables in all – are controlled

Table 1. Positive relationships between species richness/evenness and community stability

Variable of interest	Other variables controlled for	Kendall's rank correlation (τ) with community stability	*P*-value
Species richness	None	0.20	$<10^{-15}$
Species richness	Species evenness	0.15	$<10^{-15}$
Species richness	STEB	0.09	1.6×10^{-8}
Species richness	Species evenness + STEB	0.07	7.4×10^{-6}
Species evenness	None	0.16	$<10^{-15}$
Species evenness	Species richness	0.12	1.6×10^{-13}
Species evenness	STEB	0.10	3.6×10^{-10}
Species evenness	Species richness + STEB	0.08	7.0×10^{-7}

Note: The relationships between diversity and community stability remain positive and statistically significant after controlling for a host of potentially confounding variables. STEB = spatial, temporal, and environmental variables and body size: longitude, latitude, the first and last years surveyed, the number of years surveyed, the means and year-to-year standard deviations of temperature and annual precipitation, mean body mass, and the square of mean body mass – 11 variables in all.

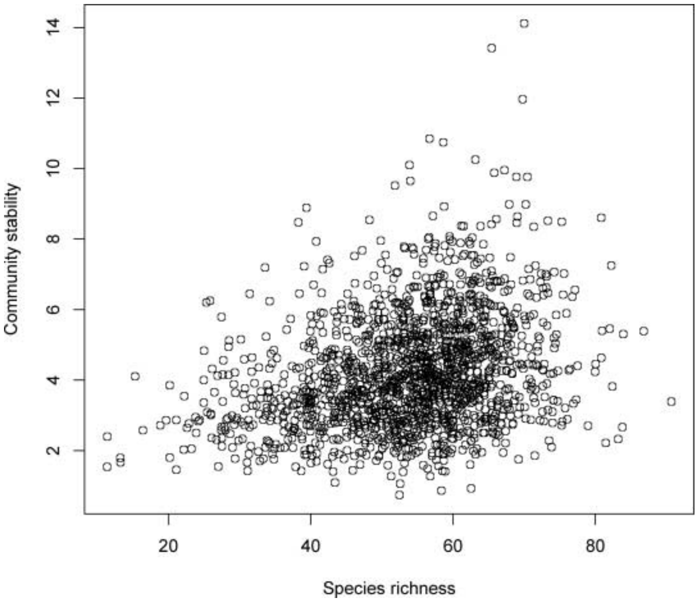

Fig. 1. Positive relationship between species richness and community stability. All of the communities with relatively few species are relatively unstable. In contrast, while some species-rich communities are also unstable, some are moderately stable and others highly stable. Overall, richness relates positively to community stability. See Table 1 for statistics.

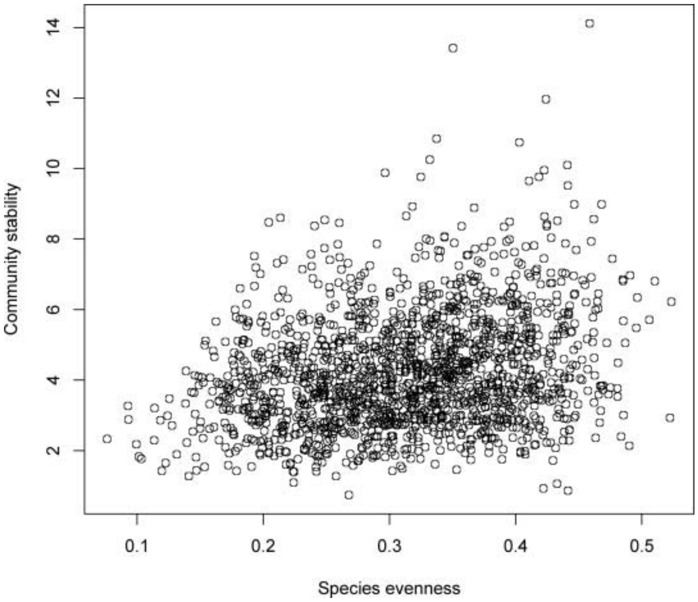

Fig. 2. Positive relationship between species evenness and community stability. As with species richness, community stability also has a quasi-triangular relationship with species evenness that is positive overall. See Table 1 for statistics.

Table 2. Relationships between species richness/evenness and the mathematical components of community stability

Variable of interest	Component of community stability	Kendall's rank correlation (τ)	P-value
Species richness	Community abundance	0.14	$<10^{-15}$
Species richness	Sum of population variances	−0.09	1.3×10^{-8}
Species richness	Sum of population covariances	0.04	0.02
Species evenness	Community abundance	−0.45	$<10^{-15}$
Species evenness	Sum of population variances	−0.59	$<10^{-15}$
Species evenness	Sum of population covariances	−0.25	$<10^{-15}$

Note: Richness relates positively to mean community abundance and summed population covariance, but negatively to summed population covariance. In contrast, evenness relates negatively to mean community abundance, and to the sums of population variances and covariances.

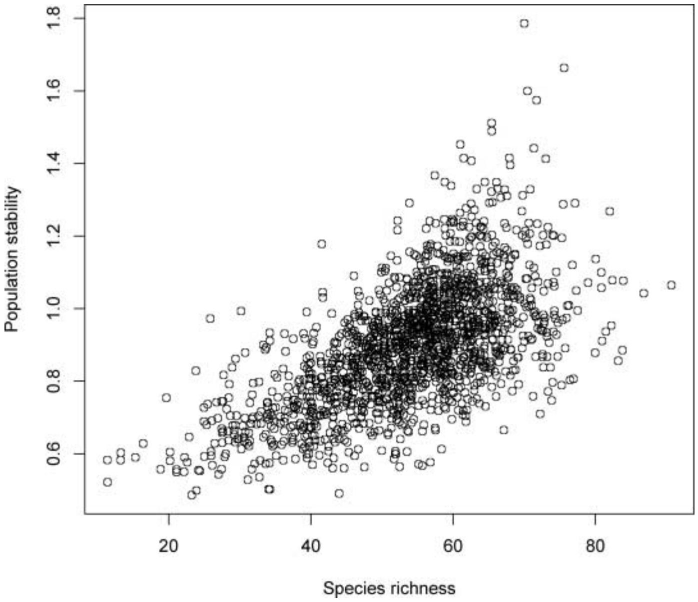

Fig. 3. Positive relationship between species richness and mean population stability. In contrast to community stability, both the minimum and the maximum of mean population stability tend to increase with species richness. See Table 3 for statistics.

for; then the rank correlation between species evenness and mean population stability, while still positive, is no longer significant. All other relationships between diversity and mean population stability also remain positive and significant when population stability is computed using de-trended abundances or when using de-zeroed abundances (see Methods).

Finally, we estimate that population stability and abundance are related as $S_P = 0.62\mu_P^{0.34}$, where S_P is the temporal stability of an individual species population and μ_P is its (temporal mean) abundance ($n = 176{,}761$; P of log-log regression $< 10^{-15}$). However, both

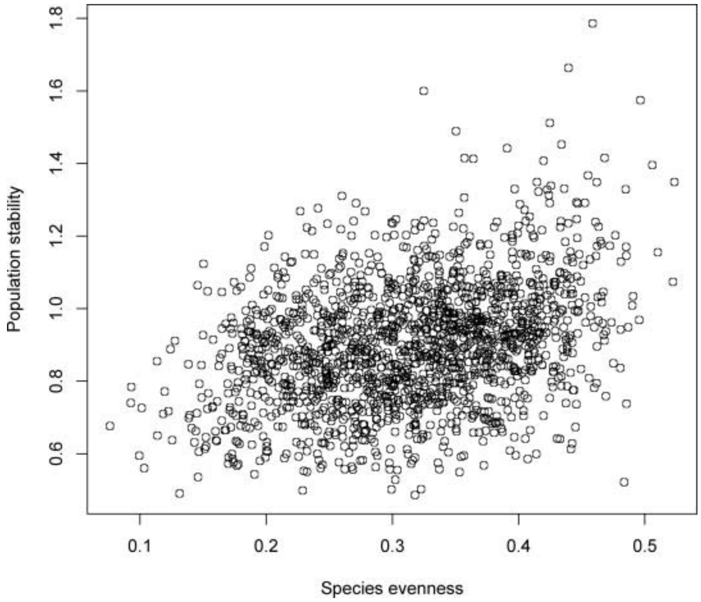

Fig. 4. Positive relationship between species evenness and mean population stability. In contrast to species richness, the maximum but not the minimum of mean population stability tends to increase with species evenness. See Table 3 for statistics.

Table 3. Positive relationships between species richness/evenness and population stability

Variable of interest	Other variables controlled for	Kendall's rank correlation (τ) with mean population stability	P-value
Species richness	None	0.44	$<10^{-15}$
Species richness	Species evenness	0.39	$<10^{-15}$
Species richness	STEB	0.33	$<10^{-15}$
Species richness	Species evenness + STEB	0.31	$<10^{-15}$
Species evenness	None	0.21	$<10^{-15}$
Species evenness	Species richness	0.14	$<10^{-15}$
Species evenness	STEB	0.10	2.3×10^{-9}
Species evenness	Species richness + STEB	0.03	0.07

Note: These results are for the mean value of population stability, taken across populations within routes. All other details are the same as in Table 1. The relationships between diversity and mean population stability remain positive, and with one exception, statistically significant after controlling for a host of potentially confounding variables.

the coefficient and the exponent of the abundance–stability equation for populations increase with increasing evenness of the communities containing those populations (all P-values $< 10^{-15}$):

- Evenness ≤ 0.15: $S_P = 0.54\mu_P^{0.29}$ ($n = 3045$)
- $0.15 <$ Evenness ≤ 0.30: $S_P = 0.60\mu_P^{0.32}$ ($n = 70{,}722$)
- $0.30 <$ Evenness ≤ 0.45: $S_P = 0.64\mu_P^{0.36}$ ($n = 97{,}588$)
- Evenness > 0.45: $S_P = 0.68\mu_P^{0.39}$ ($n = 5406$)

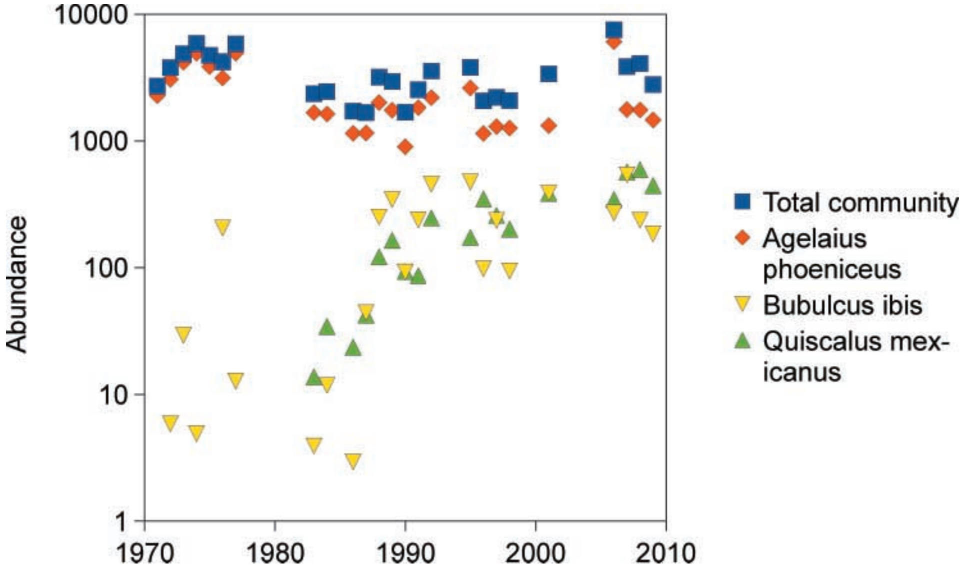

Fig. 5. A low-diversity, low-stability community. Breeding Bird Survey (BBS) Route 14.150 (Brawley, California). Species richness = 30.40, species evenness = 0.08, community stability = 2.33, mean population stability = 0.68. Only the three most abundant species along this route, plus the multi-species community as a whole, are shown.

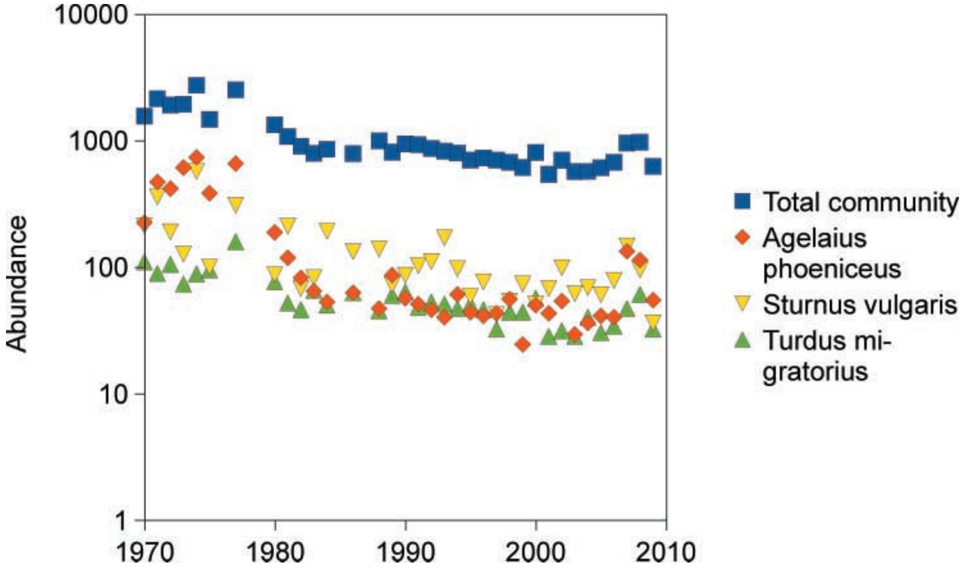

Fig. 6. A high-diversity, low-stability community. Breeding Bird Survey (BBS) Route 72.33 (Bow Bridge, Pennsylvania). Richness = 71.49, evenness = 0.29, community stability = 1.86, mean population stability = 0.99. Only the three most abundant species, plus the multi-species community as a whole, are shown.

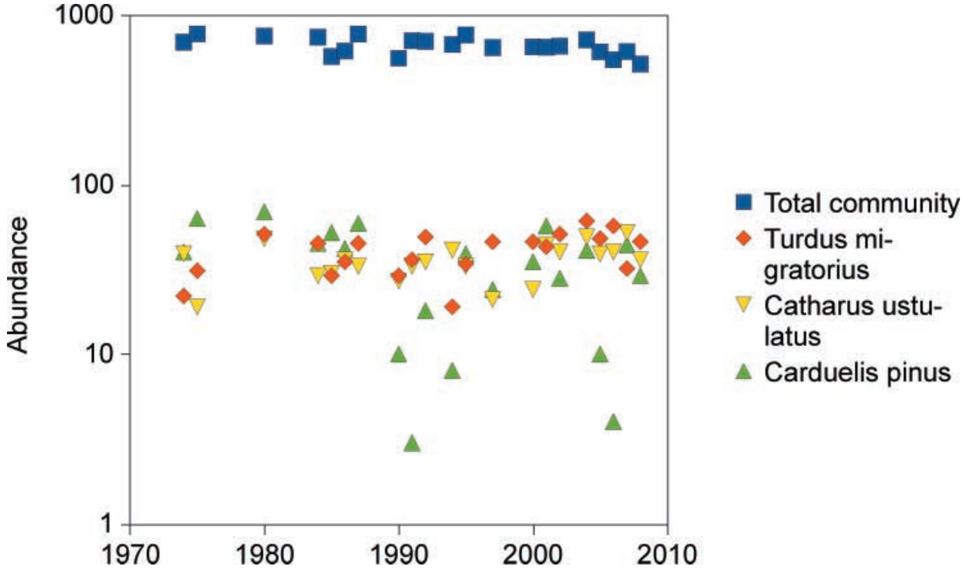

Fig. 7. A high-diversity, high-stability community. Breeding Bird Survey (BBS) Route 11.409 (Brookmere, British Columbia). Richness = 73.33, evenness = 0.43, community stability = 8.52, mean population stability = 1.22. Only the three most abundant species, plus the multi-species community as a whole, are shown.

DISCUSSION

The findings reported here yield strong field support for the hypothesis that species richness enhances temporal stability at the community level. Thus we have extended the domain in which richness and community stability are known to co-vary, from small-scale experimental settings to large-scale natural ecosystems. And we have greatly enlarged the number of communities analysed – by two to three orders of magnitude compared with previous experiments – as well as expanding the number of species examined per community.

Second, our results also extend the known domain of the diversity–community–stability relation from the number of species alone to species evenness as well. Previous studies have mostly focused on richness, and neglected evenness. One of the few salient experiments reported to date failed to indicate any effect of evenness on temporal stability (Isbell *et al.*, 2009), although another experiment did indicate a positive effect of evenness on the stability of net ecosystem denitrification (Wittebolle *et al.*, 2009). Our observational results should help to motivate additional experimental, observational, and theoretical studies of evenness–stability relations.

Our third major result is an intriguing contrast between the way richness and evenness relate to the mathematical components of community stability. The strong positive link between richness and community abundance, compared with the weaker links between richness and summed population variances and covariances, suggests over-yielding (rather than portfolio or covariance effects) as the primary driver of the richness–community-stability relationship. In contrast, the strong negative relationships between evenness and all three components of community stability suggest that evenness boosts community stability through both portfolio and covariance effects, despite having an *under*-yielding effect on community abundance. The estimated link between species richness and community abundance may be inflated by the fact that communities with higher observed total abundances tend to have more complete lists of species (Rosenzweig *et al.*, 2010). Nevertheless, it remains a question for future research why richness and evenness should enhance community stability through such disparate pathways.

Fourth, we found that species richness and evenness also relate positively to temporal stability at the population level. Three leading ecologists hypothesized a positive diversity–population-stability relationship in the 1950s (Odum, 1953; MacArthur, 1955; Elton, 1958). But early empirical tests of this hypothesis yielded a confusing mix of positive, negative, and ambiguous results (Goodman, 1975), and more recent experimental studies have also produced mixed results (Romanuk *et al.*, 2006; Tilman *et al.*, 2006). Our analysis – perhaps the largest undertaken to date – indicates that Odum, MacArthur, and Elton may have been right after all.

As Figs. 1 and 2 show, the maximum, but not the minimum, of community stability greatly increases with species richness and evenness. Figures 5, 6, and 7 represent sample BBS routes near the three corners of these quasi-triangular relationships between diversity and community stability. These relationships indicate that diversity is a necessary but not a sufficient condition for community stability. The same appears to be true when it comes to evenness as a condition for mean population stability (Fig. 4). However, both the maximum and the minimum of mean population stability increase with increasing richness (Fig. 3). The triangular relationships shown in Figs. 1, 2, and 4 raise further questions for future research. What determines whether a species-rich community has high or low community stability? And what distinguishes the highly even communities that also have high population or community stability from those that have low stability?

Finally, we confirmed that Taylor's Law can explain part of the positive relationship between species evenness and mean population stability among North American birds. Just as that law predicts, population stability has a positive relationship with population abundance but with strongly diminishing returns. This in turn implies that mean population stability should be higher in more even communities. But we also found evidence for an additional positive effect of evenness on population stability beyond what Taylor's Law can explain by itself. Taylor's Law explains the increase of mean population stability with evenness in terms of the fact that, other things being equal, more even communities comprise populations at more moderate levels of abundance (see the Introduction). But it does not explain why more even communities also have higher population stability for any given level of population abundance, as evidenced by the equations at the end of the Results section.

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REFERENCES

Chapin, F.S., III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M. 2000. Consequences of changing biodiversity. *Nature*, **405**: 234–242.

Diamond, J.M. 1986. Overview: laboratory experiments, field experiments, and natural experiments. In *Community Ecology* (J.M. Diamond and T.J. Case, eds.), pp. 3–22. New York: Harper & Row.

Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen.

Goodman, D. 1975. The theory of diversity–stability relationships in ecology. *Q. Rev. Biol.*, **50**: 237–266.

Isbell, F.I., Polley, H.W. and Wilsey, B.J. 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett.*, **12**: 443–451.

Ives, A.R. and Carpenter, S.R. 2007. Stability and diversity of ecosystems. *Science*, **317**: 58–62.

Kilpatrick, A.M. and Ives, A.R. 2003. Species interactions can explain Taylor's power law for ecological time series. *Nature*, **422**: 65–68.

Lehman, C.L. and Tilman, D. 2000. Biodiversity, stability, and productivity in competitive communities. *Am. Nat.*, **156**: 534–552.

MacArthur, R.H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology*, **36**: 533–536.

Mikkelson, G.M. 2009. Diversity–stability hypothesis. In *Encyclopedia of Environmental Ethics and Philosophy* (J.B. Callicott, R. Frodeman, V. Davion, B.G. Norton, C.Palmer and P.B. Thompson, eds.), Vol. 1, pp. 255–256. Farmington Hills, MI: Macmillan.

Odum, E.P. 1953. *Fundamentals of Ecology*. Philadelphia, PA: W.B. Saunders.

Peters, R.H. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University.

Pimm, S.L. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species Communities*. Chicago, IL: University of Chicago Press.

Pimm, S.L. and Redfearn, A. 1988. The variability of population densities. *Nature*, **334**: 613–614.

Romanuk, T.N., Vogt, R.J. and Kolasa, J. 2006. Nutrient enrichment weakens the stabilizing effect of species richness. *Oikos*, **114**: 291–302.

Rosenzweig, M.L., Donoghue, J., II, Li, Y.M. and Yuan, C. 2010. Estimating species density. In *Biological Diversity: Frontiers in Measurement and Assessment* (A. Magurran and B.J. McGill, eds.), pp. 276–288. New York: Oxford University.

Sauer, J.R., Hines, J.E. and Fallon, J. 2008. *The North American Breeding Bird Survey*. Laurel, MD: USGS Patuxent Wildlife Research Center.

Smith, B. and Wilson, J.B. 1996. A consumer's guide to evenness indices. *Oikos*, **76**: 70–82.

Taylor, L.R. and Woiwod, I.P. 1980. Temporal stability as a density-dependent species characteristic. *J. Anim. Ecol.*, **49**: 209–224.

Tilman, D., Reich, P.B. and Knops, J.M.H. 2006. Biodiversity and stability in a decade-long grassland experiment. *Nature*, **441**: 629–632.

Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K. *et al.* 2009. Initial community evenness favours functionality under selective stress. *Nature*, **458**: 623–626.