

AN EMPIRICAL EVALUATION OF THE INSURANCE HYPOTHESIS IN DIVERSITY–STABILITY MODELS

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Abstract. An important stabilizing mechanism in most diversity–stability models is the insurance hypothesis, which involves correlation/covariance relationships among species. These models require that species do not fluctuate synchronously over time: that is, the correlation between pairs of species does not equal 1.0. However, the strength of this stabilizing mechanism increases as correlations decline away from 1.0, especially as they become more negative and also as the summed covariance across all species pairs becomes more negative. We evaluated the importance of the insurance hypothesis as a stabilizing mechanism by examining a variety of terrestrial assemblages using long-term data from the Global Population Dynamics Database, the Breeding Bird Survey, and a long-term site in southeastern Arizona, USA. We identified co-occurring assemblages of species and calculated the Spearman rank correlations of all pairs of species and the summed covariance of the entire assemblage. We found that, in most assemblages, positive correlations were two to three times more common than negative and that the magnitude of the positive correlations tended to be stronger than the negative correlations. For all but three assemblages, the summed covariance was positive. Data from larger spatial scales tended to exhibit more positive correlations, but even at the smallest spatial scales, positive correlations outnumbered negative. We suggest that species often covary positively because coexisting species respond similarly to fluctuations in their resource base driven by climatic fluctuations. As such, our review suggests that the insurance hypothesis may not be a strong mechanism stabilizing fluctuations in natural terrestrial communities.

Key words: *Breeding Bird Survey; competition; covariance effect; environmental forcing; Global Population Dynamics Database; scale; temporal stability.*

INTRODUCTION

Ecologists have long sought to understand the manner in which the stability of a community is affected by its diversity (MacArthur 1955, Elton 1958). A growing body of empirical work has found that more diverse communities are more stable (i.e., exhibit smaller fluctuations over time) although such a relationship is far from universal (see Cottingham et al. 2001, Loreau et al. 2001, Hooper et al. 2005 for reviews). However, there have been fewer attempts to elucidate the mechanisms that produce such patterns (but see Tilman 1999, Petchey et al. 2002, Valone and Hoffman 2003, Bai et al. 2004, Lepš 2004, Steiner 2005, Steiner et al. 2005).

Theory suggests that diversity can enhance temporal stability via different mechanisms. A mechanism common to many diversity–stability models concerns patterns of covariation in species abundance over time (e.g., Tilman et al. 1998, Ives et al. 1999, 2000, Tilman 1999, Yachi and Loreau 1999, Hughes and Roughgarden 2000, Lehman and Tilman 2000, Loreau 2000, Ives and

Hughes 2002, Lhomme and Winkel 2002). This mechanism, called the insurance hypothesis (Yachi and Loreau 1999, Ives et al. 2000, Cottingham et al. 2001) or the covariance effect (Tilman 1999, Lehman and Tilman 2000), requires that pairs of species respond differently to environmental fluctuations so that their correlation is less than 1.0. Some authors assume that pairwise competitive interactions will often result in negative correlations (covariances; Frost et al. 1995, Tilman 1999, Hughes and Roughgarden 2000).

Examination of these models reveals that the stabilizing effect of the insurance hypothesis depends strongly on the sign and magnitude of covariance relationships (Cottingham et al. 2001). In all models, the more negative the correlations, the stronger the stabilizing effect, and the summed covariance is predicted to be negative. (Correlations are standardized covariances that range from –1.0 to 1.0.) Positive correlations destabilize community fluctuations in some models (e.g., Tilman 1999, Lehman and Tilman 2000), while they weaken, but do not eliminate, the stabilizing effect of diversity in other models (e.g., Yachi and Loreau 1999, Ives et al. 2000, Ives and Hughes 2002). Thus, the nature and magnitude of covariance relationships in communities will determine the importance of the insurance hypothesis as a stabilizing force. A prepon-

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PLATE 1. A large *Pogonomyrmex* harvester ant interacting with a smaller *Dorymyrmex*. These two competitors covary positively at the Portal site in southeastern Arizona, USA. Photo credit: Alex Wild.

derance of positive correlations in natural communities, especially those far from zero, and positive summed covariances will indicate that the insurance hypothesis does not play a strong role in stabilizing community fluctuations. A preponderance of negative correlations and negative summed covariances in natural communities will reveal its importance as a stabilizing force.

Recent reviews of the diversity–stability literature have called for empirical evaluation of the underlying assumptions of these models to provide a better mechanistic understanding of diversity–stability relationships (McCann 2000, Cottingham et al. 2001, Loreau et al. 2001, Hooper et al. 2005). Here, we do just that with respect to the insurance hypothesis by examining patterns of correlations among pairs of species and summed covariances in local assemblages that span a wide variety of terrestrial taxa. Our intent is not to attempt to tease apart whether patterns of covariation are due to competition or differential responses to environmental variation. Furthermore, we are not evaluating diversity–stability relationships per se. Instead, our intent is to determine how often pairs of species in local communities exhibit negative or positive correlations over time, to quantify their magnitudes, and to determine whether summed covariances in assemblages are positive or negative. This will allow us to characterize how often and how strongly the insurance hypothesis/covariance effect acts as a stabilizing force in natural communities.

We focus on assemblages of species or species pairs in which competition is known or suspected to be strong by focusing on species that are trophically and morphologically similar. We do this because some diversity–stability models assume competition occurs in communities (e.g., Lehman and Tilman 2000, Ives and Hughes 2002) and because competition is assumed to produce negative covariation between species. In addition, because most empirical studies of diversity–stability relationships have been conducted in grasslands or microcosms (Cottingham et al. 2001), one goal of our work was to survey a wide diversity of taxa from natural terrestrial communities.

MATERIALS AND METHODS

We obtained data from three sources: published studies from the Global Population Dynamics Database (GPDD; Natural Environment Research Council, Centre for Population Biology, *available online*),⁴ the Breeding Bird Survey (BBS), and from a long-term study of rodents and ants from a single study site in southeastern Arizona, USA. The GPDD is a compilation of >5000 population time series. We sorted the database by taxa and searched for studies that: (1) contained multiple trophically similar species that presumably compete for resources, (2) spanned at least

⁴ (<http://cpbnts1.bio.ic.ac.uk/gpdd>)

TABLE 1. Summary of the Global Population Dynamics Database analyses.

Group/taxon	No. species/assemblage	No. years	Correlations			Σ covariance	Scale (ha)
			Total	Positive (%)	Median		
Alaskan raptors ¹	3	12	3	66.7	0.21	67	unknown
Saskatchewan dabblers ²	7	26	21	100	0.53	83 970	1288
North Dakota dabblers ³	7	17	21	90.5	0.37	2855	1231
Wytham woods rodents ⁴	2	20	1	100	0.55	423	94
Russian shrews ⁵	6	11	15	73.3	0.25	37	unknown
Utah snakes ⁶	2	11	1	100	0.67	3274	1 den
Dutch beetles ⁷	2	27	1	100	0.69	0	625
UK odonates ⁸	5	25–27 (26.4)†	10	70.0	0.16	2402	2
Argentinian grasses ⁹	7	9	21	52.3	0.0	8	1
Argentinian asters ⁹	3	13	3	33.3	–0.17	0	1
UK butterflies ¹⁰							
Whites	3	10	3	100	0.59	813	45
Blues	3	10	3	66.7	0.07	18 509	45
Skippers	2	10	1	100	0.31	5799	45
Hubbard Brook birds ¹¹							
All species	19	16	171	57.8	0.11	732	10
Bark foragers	3	16	3	66.7	0.32	1	10
Foliage gleaners	9	16	36	52.2	0.06	116	10
Ground foragers	7	16	21	61.9	0.19	40	10

Note: Sources are indicated by superscripted numerals: 1, Mindell et al. (1987); 2, Vickery and Nudds (1984); 3, Higgins et al. (1992); 4, Southern (1970); 5, Sheftel (1989); 6, Julian (1951); 7, Van Dijk and Den Boer (1992); 8, Moore (1991); 9, E. Chaneton, K. Ronaldo, and J. C. Leon (*unpublished data*); 10, Pollard (1991); 11, Holmes et al. (1986).

† The value in parentheses is the mean of multiple data sets; for this, the range of years is given.

10 years, and (3) were conducted at relatively small scale (1 to <1300 ha). We included one nine-year study to increase the number of plant assemblages, and we consulted the original papers or authors to determine the scale of the study.

The BBS is a standardized census of breeding birds in the United States and Canada that has been conducted since 1966. The census is comprised of individual census routes 39 km in length. Observers record the abundance of each species seen or heard in a 3-min period and within 400 m of a location at 50 stops spaced 0.8 km apart along the route (Sauer et al. 2005). We identified sympatrically breeding pairs and small groups of species (assemblages) that have been identified in the literature as strong competitors or are presumed competitors based on trophic or nesting similarity. We then identified routes that contained these species and eliminated all routes that did not have at least 10 years of data and a mean of five or more individuals per species over the time period analyzed. For our analyses, we calculated the correlation structure for each pair of species for all routes examined.

Finally, we used data from a study site near Portal, Arizona, which has recorded the abundance of rodents and ants in standardized surveys since 1977 (Brown 1998). The Portal site (20 ha) contains 24 0.25-ha experimental plots subjected to various manipulations of rodents and ants. Rodents are censused on each plot monthly; ants are censused yearly.

With the Portal rodent data, we examined the cross-correlation in mean yearly abundance among pairs of species using data from all 24 experimental plots. Mean yearly abundances were calculated from monthly trapping on each plot from 1978 to 2005 for the nine

most common seed-eating species (*Dipodomys spectabilis*, *D. ordii*, *D. merriami*, *Chaetodipus baileyi*, *C. penicillatus*, *Perognathus flavus*, *Peromyscus eremicus*, *P. maniculatus*, and *Reithrodontomys megalotis*) and three common omnivores (*Onychomys torridus*, *O. leucogaster*, and *Neotoma albigula*).

We focused on the six most common ant species at the Portal site (Valone and Kaspari 2005): four granivores (*Pheidole tucsonica*, *P. rugulosa*, *Pogonomyrmex desertorum*, *Solenopsis invicta*) and two omnivores (*Forelius cf. pruinosis* and *Dorymyrmex insanus*; see Plate 1). We used data collected from 1977 to 2002 from eight plots on which ant and seed abundances were not manipulated.

For all assemblages, we carried out Spearman rank correlations on the abundance of species pairs over time (because population data are unlikely to be normally distributed) and calculated the summed covariance of the entire assemblage. Years of zero abundance for a particular species in any data set were included in all analyses although such occurrences were rare. We do not report significance values for any single relationship because we were interested in the overall patterns of positive and negative associations. For each assemblage, we tabulated the number of correlations in 0.2-unit bins ranging from –1.0 to 1.0. We plotted these for all data sets with >10 correlations. For the smaller data sets, summary values (percentage of positive correlations, median correlation) are reported.

RESULTS

We identified 12 studies from the GPDD that met our criteria. The scale of these studies ranged from 1 m² to 1231 ha (Table 1; Appendix A) and included birds,

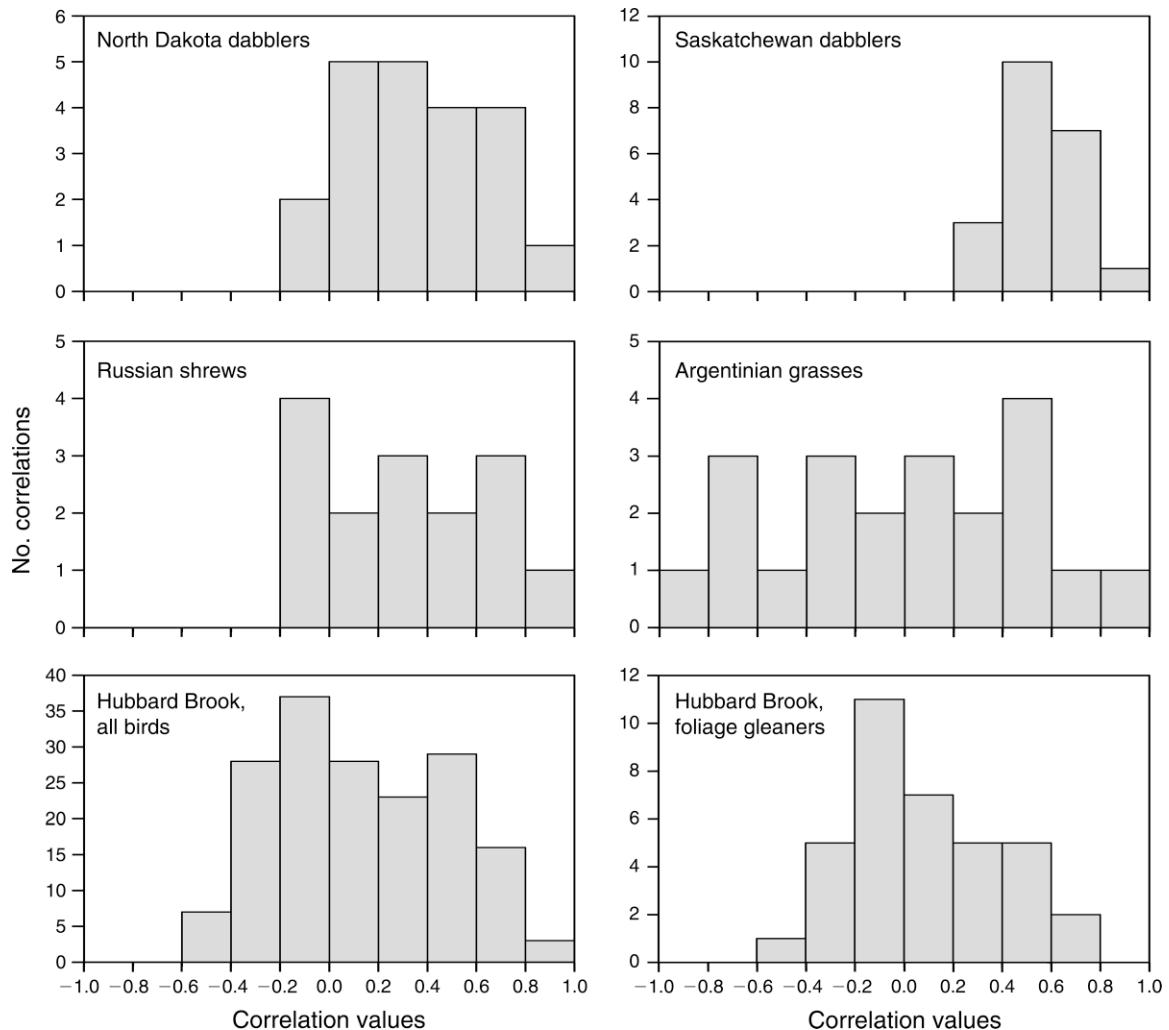


FIG. 1. The distribution of species pair correlation coefficients for six groups of Global Population Dynamics Database data: North Dakota dabblers, Saskatchewan dabblers, Russian shrews, Argentinian grasses, all Hubbard Brook birds, and Hubbard Brook foliage-gleaning birds only.

mammals, insects, reptiles, and plants. Assemblages contained 2–22 species in studies ranging from 9 to 27 years.

All GPDD communities except one exhibited more positive than negative correlations in abundance between pairs of species (33.3–100% positive correlations) with an average median correlation of 0.26 for the 12 groups. Over all of the GPDD analyses, there was a positive relationship between the scale of the study and the percentage of positive correlations observed (Spearman rank correlation, $r = 0.89$, $P = 0.001$; Appendix B).

Examination of Table 1 reveals that the two dabbling-duck assemblages and the shrew assemblage were dominated by moderately strong positive correlations (median correlations of 0.53, 0.37, and 0.25, respectively; Fig. 1). In addition, the three two-species assemblages (Wytham woods rodents, Utah snakes, and Dutch beetles) also had large positive correlations (0.55, 0.67,

and 0.69, respectively; Table 1). In contrast, the two Argentinian plant assemblages were not dominated by positive correlations. The aster assemblage was the only one with a negative median correlation (-0.17), while the median correlation for the grass assemblage was zero (Table 1, Fig. 1). The UK odonates fell between the above groups with 70% positive correlations but a median correlation of only 0.16. None of the GPDD assemblages had a negative summed covariance, although four assemblages had a summed covariance close to 0.

The Hubbard Brook bird community was sufficiently large to perform analyses on both the entire bird community and three subsets of species that we considered to be strong competitors (the bark foragers, the foliage gleaners, and the ground foragers). For the entire assemblage, the median correlation was 0.11. For the three foraging guilds, the median correlations were

TABLE 2. Summary of the Breeding Bird Survey analyses.

Group/taxon	No. species	No. years†	Correlations			No. routes	Σ covariance
			Total	Positive (%)	Median		
Woodpeckers and starlings ¹	2–4	12–32 (20.8)	32	68.7	0.16	9	1348
Kingbirds ²	2	12–30 (18.9)	10	80.0	0.36	10	294
Flycatchers ³	2–3	12–39 (23.0)	16	56.3	0.05	6	58
Chickadees ⁴	2	11–35 (16.9)	7	85.7	0.19	7	32
Kinglets ⁵	2	10–18 (12.2)	5	80.0	0.37	5	66
MacArthur's Warblers ⁶	2–4	14–30 (21.3)	70	94.2	0.37	9	1800
Understory warblers‡	2–6	11–36 (18.5)	48	72.9	0.14	12	438
Icterids ⁷	2	11–36 (20.8)	5	80.0	0.34	5	25612
Cavity nesters ⁸	4–6	11–37 (18.6)	96	69.8	0.19	8	9194
Western foliage gleaners ⁹	2–3	11–29 (17.3)	10	90.0	0.52	6	149
Flycatchers/redstarts ¹⁰	2	15–39 (23.9)	11	90.9	0.48	11	144
Nuthatches/warblers ¹¹	2	12–30 (20.4)	5	80.0	0.16	5	82

Note: Sources (for competition data) are indicated by superscripted numerals: 1, Troetschler (1976), Sedgwick and Knopf (1990), Kerpez and Smith (1990), Ingold (1994, 1998), Wiebe (2003); 2, Murphy (1987); 3, Johnston (1971); 4, Smith (1967), Minock (1972), Hill and Lein (1988); 5, Franzreb (1984); 6, Morse (1967a, 1971, 1976), Sabo and Holmes (1983); 7, Rutledge and Chandler (1979); 8, Pogue and Schnell (1994), Radunzel et al. (1997); 9, Rusterholz (1981); 10, Sherry (1979), Martin et al. (1996); 11, Morse (1967b).

† Values in parentheses are means of multiple data sets; ranges of years are given.

‡ Sympatric breeders, trophic similarity.

0.32, 0.06, and 0.19, respectively. A visual comparison of the distribution of correlations for the entire community compared to one of the guilds (foliage gleaners) reveals little difference (Fig. 1).

Using the BBS data, we identified 12 assemblages of presumed competitors from 93 routes across North America that included insectivores, granivores, and cavity nesters. Assemblages contained two to six species censused on 5–12 routes over 10–39 years (Table 2; Appendix C).

In all but one BBS assemblage, positive correlations outnumbered negative by more than two to one (Table 2). The percentage of positive correlations ranged from 56.3% to 94.2%, with the average median of 0.26. MacArthur's Warblers exhibited the most positive correlations (94.2% positive, median correlation = 0.37), while the three groups with the fewest positive correlations (woodpecker/starling, flycatchers, and cavity nesters) had median correlations of 0.16, 0.05, and 0.19, respectively. In most of the BBS assemblages, most correlations were strongly positive while a few species pairs exhibited strong negative correlations (Fig. 2). All of the BBS assemblages had positive summed covariances, and most were far from 0.

At the Portal site, >65% of the correlations among rodent species pairs were positive (Table 3) with a median correlation of 0.12. Analyses of just the nine seed-eating rodents revealed a similar pattern: 66.7% positive correlations with a median correlation of 0.12. The Portal rodent data resembled many of the BBS data sets: a few strong negative correlations existed but these were rare relative to the positive correlations, and many of the positive correlations were >0.6 (Fig. 3). Summed covariances were positive.

The Portal ant community only exhibited positive correlations. The median correlation for all species pairs was 0.45, while it was 0.49 for just the four species of

seed-eating ants (Table 3), and the summed covariances were positive.

DISCUSSION

Our goal was to evaluate the relative importance of the insurance hypothesis by characterizing correlation and summed covariance relationships in a wide range of natural communities. Most diversity–stability models assume that pairs of species will exhibit differential responses to environmental fluctuations such that their correlations in abundance will not be 1.0. Not surprisingly, we found all pairs of species exhibited correlations <1.0. However, the strength of stabilizing effect of the insurance hypothesis increases as correlations decline from 1.0 (Yachi and Loreau 1999, Ives et al. 2000, Ives and Hughes 2002) and becomes stronger when correlations and summed covariances are negative (Cottingham et al. 2001). We found that most pairs of species in natural communities exhibited positive rather than negative correlations. In nearly all communities, positive correlations were two to three times more abundant than negative correlations and summed covariances were positive. Our data therefore suggest that the insurance hypothesis may not be a strong factor that stabilizes fluctuations in these communities. Indeed, in the diversity–stability models of Tilman and coworkers (Tilman 1999, Lehman and Tilman 2000), positive correlations among pairs of species destabilize community fluctuations (see also McCann 2000, Lhomme and Winkel 2002, DeWoody et al. 2003).

Results from the GPDD studies, the BBS data, and from the Portal site in Arizona produced quite similar patterns despite wide variation in taxa and sampling methods: pairs of species covary positively more often than negatively and summed covariances are positive. This is true despite the fact that species abundance data reviewed here come both from actual counts and indices of abundance. Abundances can be difficult to estimate

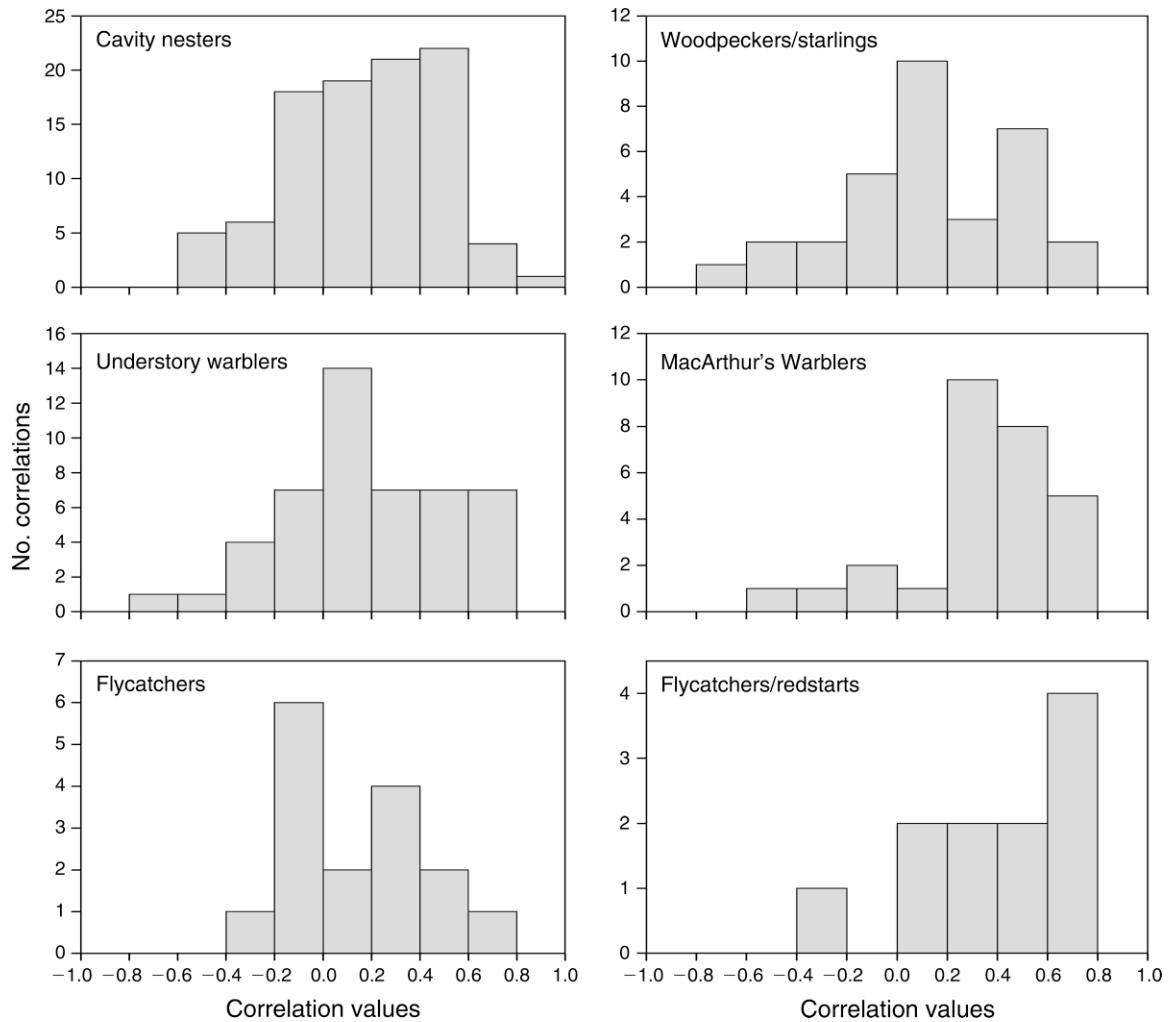


FIG. 2. The distribution of species pair correlation coefficients for six groups of Breeding Bird Survey birds: cavity nesters, woodpeckers/starlings, understory warblers, MacArthur's Warblers, flycatchers, and flycatchers/redstarts.

(e.g., Williams et al. 2002), and the BBS abundance data relies on volunteers, which can bias results (e.g., Kendall et al. 1996). Thus, it is reassuring that the correlation and summed covariance patterns observed in the BBS data are similar to those derived from actual counts (e.g., Portal data): potential problems associated with the use of indices and volunteer observers appear to be minimal.

Some of the best support for the insurance hypothesis comes from the plant assemblages. In one of the two Argentinian plant assemblages examined, negative correlations outnumbered positive and the summed covariance was zero. Other work on plant communities provides additional support for the insurance hypothesis. Both Tilman (1999) and Bai et al. (2004) suggested that covariance relationships were important factors stabilizing fluctuations in the plant communities they studied, and Houlahan et al. (2007) reported that three plant communities they examined had fewer positive covariances than would be expected by chance. Thus,

the insurance hypothesis may be an important stabilizing mechanism in some plant communities, but additional work is needed. Plants can compete strongly for limiting resources (e.g., Grover 1997) and can also respond differentially to environmental fluctuations (e.g., Adler et al. 2006), two mechanisms that can enhance negative covariance relationships. Less clear, however, is why negative correlations and summed covariances were not especially common in the plant assemblages examined and why they were much more rare in the animal communities examined.

Houlahan et al. (2007) recently conducted a similar meta-analysis that examined the prevalence of negative covariances in 19 communities of presumed competitors, although they did not include any bird communities. They reported the proportion of sampling units (e.g., plots) in which a community exhibited negative covariances rather than actual correlations between pairs of species. Their results parallel those reported here: most communities exhibited positive rather than negative

TABLE 3. Summary of analyses from the Portal, Arizona, USA, site.

Group/taxon	No. species	No. years	Correlations			Σ covariance
			Total	Positive (%)	Median	
Seed-eating rodents	9	23	36	66.7	0.12	212
All rodents	11	23	66	65.1	0.12	392
Seed-eating ants	4	19	6	100	0.49	107
All ants	6	19	15	100	0.45	206

Note: In each case, site was the scale at which the analyses occurred.

covariances. They also found that as the scale of the sampling unit increased, so did the proportion of positive covariances.

In studies that examine the effect of competition on community dynamics, spatial scale must be sufficiently small to allow competitive interactions to play out (e.g., Mack and Harper 1977, Naeem et al. 2000, Van de Koppel et al. 2006). That said, it can be difficult to determine the appropriate scale for a particular taxon. In the combined meta-analyses (Houlahan et al. 2007 and the present study), organisms ranged from small-bodied odonates and herbaceous plants to large-bodied birds and trees and the size of the sampling unit generally increased with organism body size. Of note, most plant studies were typically conducted at smaller spatial scales than animal studies. This may, in part, help to explain why so few animal studies exhibited negative covariances. Additional work is required over a broader range of spatial scales to better evaluate the effect of scale on covariance relationships.

However, we believe that inappropriate spatial scale cannot, in itself, account for the preponderance of positive covariances reported here and in Houlahan et al. (2007) because even those plant and animal communities censused at the smallest spatial scales exhibited significantly more positive than negative covariances and correlations. We agree with Houlahan et al. (2007) that such results suggest that environmental forcing (i.e., year-to-year fluctuations in climatic conditions such as precipitation and temperature) likely helps to synchronize the dynamics of interspecific competitors within local assemblages (Sabo 2005). Large-scale climatic fluctuations are known to synchronize intraspecific population dynamics over large spatial scales (Post and Forchhammer 2002). At more local scales, species using similar resources should be positively and negatively affected together by fluctuations in their resource base. Indeed, Kaspari and Valone (2004) found that the abundance of all granivorous ants at the Portal site was strongly and positively affected by summer precipitation, which affects their resource base, the seeds of summer annual plants. Thus, we suggest that similar responses to environmental fluctuations promote positive covariation in abundance for species pairs in many communities (cf. Dunning and Brown 1982).

Note that our interpretation does not imply that competition is a weak force structuring local communities. Numerous studies have shown that competition is

an important force affecting the abundance of species (Begon et al. 2006). Indeed, results from removal experiments at the Portal site have demonstrated strong competition between large- and small-bodied rodents at the site (Valone and Brown 1995) and between ant species (Valone and Kaspari 2005). Yet, despite this, most large- and small-bodied rodents at the site and all ants exhibited positive covariances and correlations in abundance (Table 3; Brown and Heske 1990). This suggests that the effect of competition may be strongest within years while environmental forcing plays a stronger role in affecting year-to-year population dynamics.

Only a handful of studies have examined the insurance hypothesis in the context of diversity–stability relationships, and similar to our work, most have failed

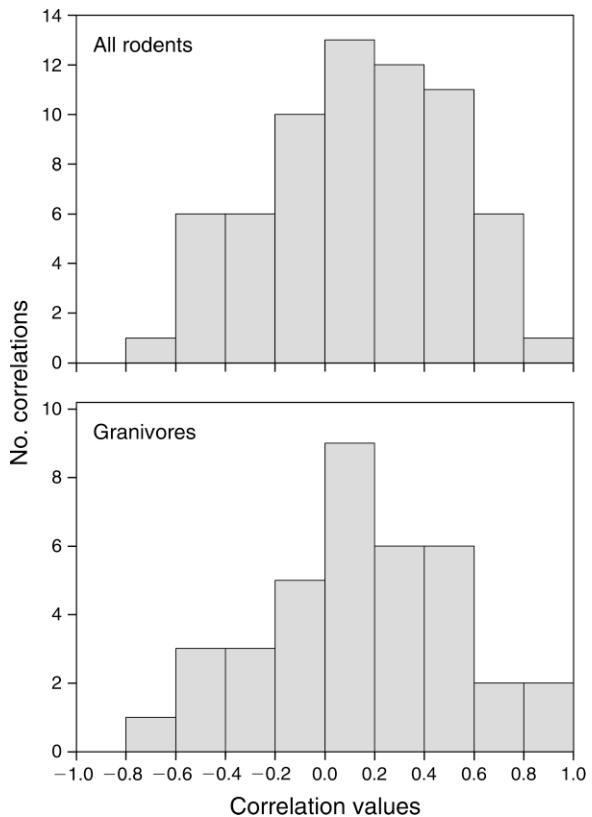


FIG. 3. The distribution of species pair correlation coefficients for rodents from the Portal, Arizona, USA, site: all rodents and only granivorous rodents.

to find strong negative covariance relationships. For instance, two studies have reported positive summed covariances that increased with richness in plant communities (Valone and Hoffman 2003, Caldeira et al. 2005), and three studies of aquatic microcosms found that covariances did not differ from zero and did not become more negative as community richness increased (Steiner 2005, Steiner et al. 2005, Vogt et al. 2006). While Tilman (1999) did report negative summed covariances in perennial plant assemblages that contained fewer than 10 species, he found that these covariances became positive rather than more negative as community richness increased.

In contrast, Petchey et al. (2002) did find a preponderance of negative covariances in microcosm communities and summed covariances became more negative as community richness increased. In addition, Bai et al. (2004) reported significant compensatory effects in perennial plant assemblages, i.e., species exhibited negative cross-correlations over time (Bai et al. 2004). Such patterns were interpreted as resulting from either differential responses to environmental fluctuations or competition (Bai et al. 2004). Inspection of the data in Bai et al. (2004), however, reveals that in the communities studied, significant positive correlations were more than twice as common as significant negative correlations, a pattern consistent with the studies reviewed here. Other workers have reported similar compensatory effects that would lend further support to the insurance hypothesis (e.g., McNaughton 1977, Tilman and Downing 1994, Naeem and Li 1997), but these could not be evaluated further because cross-correlations or data were not reported. Thus, while the insurance hypothesis is a key element of most diversity–stability models and may be an important stabilizing force in some plant communities, its importance as a general stabilizing mechanism lacks widespread, empirical support (Steiner et al. 2005).

We want to emphasize that our work is not an evaluation of diversity–stability models, nor is it an explicit test of the insurance hypothesis. That would require both a direct evaluation of the manner in which different species respond similarly or differently to environmental conditions and an examination of covariance relationships across a range of community diversities. In lieu of such data, we attempted to investigate a key aspect of the insurance hypothesis, that pairs of species will exhibit negative covariance due to either competition or differential responses to environmental fluctuation, by examining the manner in which population sizes covary, which we believe is a reasonable surrogate.

Because we find that most pairs of species tend to covary positively rather than negatively, our work suggests that the insurance hypothesis likely does not strongly stabilize fluctuations in many terrestrial communities. Thus, we suggest that it might be profitable to focus attention on other potential stabilizing mecha-

nisms. One that may hold promise is overyielding, which occurs when a total community property such as total abundance or biomass increases with diversity (Tilman 1999, Lehman and Tilman 2000). There is growing evidence that overyielding is an important mechanism in the explanation of the positive relationship between diversity and productivity in many systems (Tilman et al. 2001, Lambers et al. 2004, Roscher et al. 2005, Zhang and Zhang 2006). In addition, overyielding has been shown to be an important stabilizing mechanism in annual plants at the Portal site (Valone and Hoffman 2003). We suggest that greater attention, both theoretical and empirical, should be placed upon this and other mechanisms to understand diversity–stability patterns.

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APPENDIX A

A list of species assemblages from the Global Population Dynamics Database (*Ecological Archives* E089-027-A1).

APPENDIX B

A figure showing the relationship between the scale of a study and the percentage of positive pairwise correlations observed for the Global Population Dynamics Database (*Ecological Archives* E089-027-A2).

APPENDIX C

A list of the Breeding Bird Survey species pairs analyzed (*Ecological Archives* E089-027-A3).