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Conserving and promoting evenness: organic farming and fire-based wildland management as case studies

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Abstract. Healthy ecosystems include many species (high richness) with similar abundances (high evenness). Thus, both aspects of biodiversity are worthy of conservation. Simultaneously conserving richness and evenness might be difficult, however, if, for example, the restoration of previously absent species to low densities brings a cost in reduced evenness. Using meta-analysis, we searched for benefits to biodiversity following adoption of two common land-management schemes: the implementation of organic practices by farmers and of controlled burning by natural-land managers. We used rarefaction to eliminate sampling bias in all of our estimates of richness and evenness. Both conservation practices significantly increased evenness and overall abundance across taxonomic classifications (arthropods, birds, non-bird vertebrates, plants, soil organisms). Evenness and richness varied independently, leading to no richness–evenness correlation and no significant overall change in richness. Demonstrating the importance of rarefaction, analyses of raw data that did not receive rarefaction indicated misleadingly strong benefits of organic agriculture and burning for richness while underestimating true gains in evenness. Both organic farming and burning favored species that were not numerically dominant, re-balancing communities as uncommon species gained individuals. Our results support the assertion that richness and evenness capture separate facets of biodiversity, each needing individual attention during conservation.

Key words: abundance; agriculture; biodiversity; conservation; ecosystem management; evenness; fire; metadata; organic farming.; species richness.

Introduction

The relationship between biodiversity and ecosystem functioning has received much recent attention (Chapin et al. 2000, Loreau et al. 2001, Cardinale et al. 2006). Experimental studies have shown that greater richness consistently increases community-wide biomass production, resource consumption, decomposition, and other desirable ecosystem properties (Loreau et al. 2001, Cardinale et al. 2006). Evenness has been somewhat overlooked, but studies increasingly suggest that evenness provides benefits for ecosystem functioning equal to those of richness in breadth and intensity (Hillebrand et al. 2008, Wittebolle et al. 2009, Crowder et al. 2010). Thus, ecosystem health would benefit from conservation schemes capable of increasing the number of species while equalizing their relative abundances (Crowder et al. 2010). High species richness can be maintained relatively simply by targeting the needs of particular endangered species (Srivastava and Vellend 2005, Benayas et al. 2009). The conservation and promotion of greater evenness has received less attention, although it is clear that particular land-use practices affect evenness (e.g., Tylianakis et al. 2007, Hillebrand et al. 2008). Evenness promotion is conceptually challenging due to the need to simultaneously rebalance densities of both rare and common species (Crowder et al. 2010), and it is not clear whether the simultaneous promotion of richness and evenness can be achieved.

A potential complication is that there is good reason to expect a negative richness–evenness relationship, with gains in one biodiversity component undermining the other. For example, management strategies that increase richness by restoring formerly absent species to low densities could skew species' relative abundances and disrupt evenness (Smith and Wilson 1996). An alternative view exists, however. Evenness and richness change might lie along a continuum, with declines in sensitive species leading first to a decrease in evenness and eventually, through extinction, a decrease in richness (Hillebrand et al. 2008). When richness and evenness are linked in this way, conservation strategies might be expected to promote both biodiversity components at once. Empirical studies in stable, unmanaged communities variously provide support for negative, neutral, or positive richness–evenness relationships (e.g., Stirling and Wilsey 2001, Ma 2005, Wilsey et al. 2005, Jarvis et al. 2008, Soininen et al. 2012). Richness–evenness relationships in managed ecosystems are similarly difficult to predict, both because the two biodiversity

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components can respond differently to the same disturbances and because conservation strategies have such wide-ranging impacts on community structure (Srivastava and Vellend 2005, Benayas et al. 2009, Svensson et al. 2012). This uncertainty calls for a synthetic examination, spanning many individual studies, of how management practices affect both richness and evenness.

We explored whether richness and evenness responded in tandem, in opposition, or independently, following implementation of two common land-use practices thought to benefit biodiversity: the adoption of organic practices in farming systems and the use of controlled burns to manage natural plant communities (see Plate 1). Purportedly, organic agriculture promotes greater richness across trophic levels (Bengtsson et al. 2005, Hole et al. 2005), with limited evidence that evenness may increase among some groups (i.e., natural enemies; Crowder et al. 2010). Likewise, in particular ecosystems, burning variously impacts richness and/or evenness (Shafi and Yarranton 1973, Whelan 1995, Battisti et al. 2008), although general patterns have not been summarized as they have for organic agriculture. As both strategies are believed to provide widespread ecological benefits (Whelan 1995, Bengtsson et al. 2005, Hole et al. 2005), we hypothesized that organic agriculture and burning would similarly benefit biodiversity across a broad range of organisms. To test these hypotheses, we compiled sets of metadata on the many published comparisons of organic vs. conventional farms, and burned vs. unburned sites. These sets of metadata were used to examine and compare how the two practices impacted interrelations among the abundance, richness, and evenness of resident microbes, plants, and animals.

Methods

Our study consisted of two components. First, we tabulated published reports comparing organic vs. conventionally managed farms, and burned vs. unburned natural areas, and calculated how richness, evenness, and total abundance changed following the adoption of the "biodiversity-friendly" practices. Second, within each set of metadata, we examined specifically how the management approaches impacted relatively rare vs. relatively common species, because any change in evenness requires species in different rank-abundance categories to respond differently.

Study selection

To identify studies comparing organic with conventional farming practices, we searched the ISI Web of Knowledge using the terms "conventional" and "organic." To identify studies comparing burned vs. unburned communities, we searched using the terms "fire" and "evenness" or "richness." Our comprehensive searches were last updated on 31 December 2011. To be included, each study had to report on the abundance of at least three taxonomic groups (at the species, genus, family, or order level) from replicated surveys. Data from each paper were obtained from figures or tables or directly from authors. We located 173 paired comparisons of organic vs. conventional farming, spanning 23 countries and 38 crops (see Appendix A and Supplement). We located 155 paired comparisons of burned vs. unburned conservation sites, spanning 21 countries (see Appendix A and Supplement). Studies in both data sets considered the following five broad taxonomic classifications: arthropods, birds, non-bird vertebrates, plants, or soil organisms. Variation in responses among eco-taxonomic groups or differences in the level of taxonomic resolution across studies could potentially impact results, and were explicitly considered in data analysis (see Appendix B).

Data collection and analysis

For each study in the metadata sets, we recorded the abundance and the observed number of taxonomic groups (richness) in the paired conventionally farmed/unburned vs. organically farmed/burned sites. Data were averaged across sample points. We next computed richness for each study using rarefaction to correct for density-based sampling biases (Gotelli and Colwell 2001). These biases can occur because, purely by chance alone, relatively rare species are more likely to be found during sampling at high- than low-density sites (Gotelli and Colwell 2001). This tends to artificially inflate richness estimates, and deflate evenness estimates, for high-density compared to low-density sites (Alatalo 1981, Gotelli and Colwell 2001).

To calculate richness for each management type in each study, we used 1000 Monte Carlo simulations in Microsoft Visual Basic (see Supplement) to construct rarefaction curves (Gotelli and Colwell 2001). Simulations drew subsamples from the survey data set to track the accumulation of taxonomic groups, and individuals within groups, by randomly sampling individuals from the surveyed communities without replacement until the density of the low-abundance management category was reached. The simulated accumulation of taxa directly provided our rarefied richness estimates for comparison. Rarefaction requires the abundance of individuals in each taxonomic group be reported (rather than a subset of sampled species). Eighty-one and 93 studies in the agriculture and burning metadata sets, respectively, met this requirement and were included (see Supplement).

Like richness, we calculated evenness using our rarefaction technique, where the accumulation of individuals in taxonomic groups was used to calculate evenness. Our evenness metric was E_{var}, chosen because it is independent of species richness and symmetric with regards to rare or dominant species (Smith and Wilson 1996):

$$E_{\mathrm{var}} = 1 - (2/\pi) \times \arctan \sum_{s=1}^{S} \left([\ln\{x_s\} - \sum_{t=1}^{S} \ln\{x_t\}/S]^2/S \right) \quad (1)$$

where x_s and x_t are the number of individuals in taxonomic group s or t, respectively, and S is the number of taxonomic groups. E_{var} is not impacted by richness or symmetry because it is based solely on variance in species' abundances, and exhibits other desirable statistical properties (Smith and Wilson 1996; see Appendix B for details and comparison with alternative metrics).

Rarefied richness and evenness values were used to calculate log response-ratio effects (Hedges et al. 1999) for organic vs. conventional farms, or burned vs. unburned sites. The log response-ratio effects were nonnormal ($P < 0.05$), and we therefore determined if they differed from 0 using Wilcoxon signed-rank tests. We next tested whether changes in richness and evenness were independent using Pearson's correlation test. In addition, we used mixed-effect models to determine if richness and evenness effects, and richness–evenness relationships, were affected by eco-taxonomic group membership or level of taxonomic resolution (see Appendix B). As 1000 rarefaction simulations were conducted for each study, variance in richness and evenness estimates across studies was minimal. Thus, we did not use weighting techniques in any of these analyses.

Evenness change requires that overall density disparities between relatively common and relatively rare species either widen (evenness decreases) or narrow (evenness increases). In our data sets, both organic farming and burning increased overall organism abundance (see *Results*), such that increasing evenness scores would be expected to reflect proportionally greater density gains by rare than common species. To verify this supposition, we calculated the relative change in abundance for groups initially in the lowest (rare), middle (average), and upper (common) third of rank abundance, when moving from conventional to organic farms, or from unburned-vegetation to burned-vegetation management sites. These values were compared using one-way ANOVA after log-transformation. A significant difference would indicate that rare, average, or common taxonomic groups benefited more from the biodiversity-friendly practices than other groups. We also determined if species detected only at organic farms or burned sites differed in a systematic way from the rarest groups that were detected under both management regimes (see Appendix B). All statistics were done in JMP (SAS Institute 2009).

Results

Both organic agriculture and burning significantly increased total organism abundance (organic, Wilcoxin signed-rank test statistic $SR^+ = 890.5$, $P < 0.0001$; burning, $SR^+ = 553.0$, $P = 0.033$) and rarefied evenness (organic, $SR^+ = 425.0$, $P = 0.030$; burning, $SR^+ = 444.5$, $P = 0.047$; Fig. 1A). However, the adoption of either practice did not significantly alter rarefied richness (organic, $SR^+ = 70.5$, $P = 0.63$; burning, $SR^+ = 358.5$, $P = 0.080$; Fig. 1A). In each metadata set, there was no

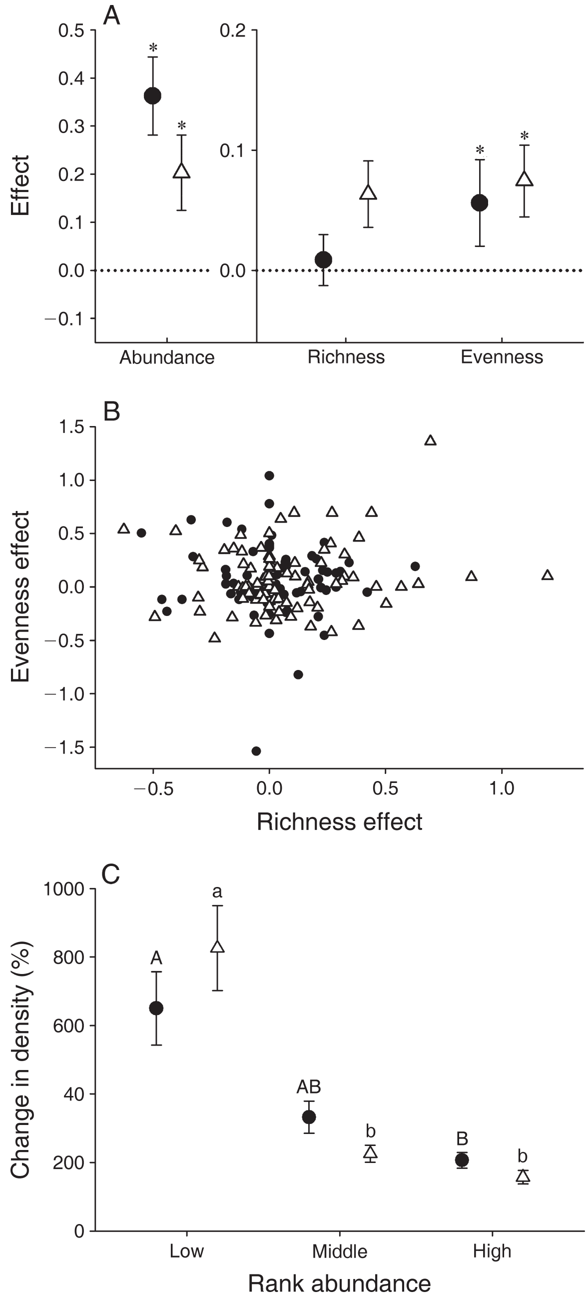

Fig. 1. Effects of moving from conventional to organic farms (solid circles) or from unburned to burned areas (open triangles). (A) The change in abundance, richness, and evenness across taxonomic classifications (arthropods, birds, non-bird vertebrates, plants, soil organisms) (mean ± SE; asterisks indicate significant effects, $P < 0.05$). (B) The relationship between change in richness and change in evenness. (C) The change in density for species among the lower, middle, and upper third of rank abundance across the same sites (letters indicate significant differences between groups: organic is shown with uppercase, and fire with lowercase letters).

evidence for correlated changes in evenness and richness (organic, $r = -0.042$, $P = 0.71$; burning, $r = 0.13$, $P = 0.21$; Fig. 1B). The patterns for increasing overall abundance and evenness, no change in richness, and no richness–evenness correlation, all were consistent across taxonomic groupings and levels of taxonomic resolution (Appendix B: Tables B3, B4).

In both metadata sets, practices that encouraged greater overall abundance and greater evenness (organic farming and burning) benefitted organisms throughout the rank-abundance continuum (Fig. 1C). However, both practices yielded significantly greater density gains to taxa in the lowest one-third of the rank-abundance continuum compared with more common taxa (Fig. 1C). Similarly, taxonomic groups only detected under the high-density management regimes joined organic and burned communities at densities roughly equal to the density gains exhibited by the rarest taxa found at both low- and high-density sites (Appendix B: Fig. B1).

Discussion

Early theory suggested that fully functioning ecosystems would be characterized by both high species richness and high evenness (De Benedictis 1973, May 1975), predictions now supported by a growing body of empirical work (Cardinale et al. 2006, Hillebrand et al. 2008). However, the lack of a broad synthetic treatment of the richness–evenness relationship during conservation has made it difficult to determine whether their simultaneous promotion is an achievable goal. We found that a taxonomically broad range of organisms similarly benefited from two commonly adopted management schemes, the implementation of organic practices in agriculture and of burning to manage natural-plant communities: Total organism abundance and rarefied evenness significantly increasing following implementation of either strategy (Fig. 1A; Appendix B: Tables B3 and B4). These evenness gains carried no cost to rarefied richness, which was not altered by either practice (Fig. 1A). Indeed, within the two sets of metadata, change in one biodiversity component was not predictive of change in the other (Fig. 1B; Appendix B: Tables B3 and B4). Our inability to find an evenness–richness correlation was not due to low statistical power, as a relatively weak correlation could have been detected (using the Pearson correlation test, values of $R^2 > 0.052$ would have been significant). This suggests that richness and evenness truly represent separate components of biodiversity, as has long been asserted (Hurlbert 1971, Stirling and Wilsey 2001, Wilsey et al. 2005, Soininen et al. 2012).

Higher species richness is often touted as a key benefit of organic farming (Bengtsson et al. 2005, Hole et al. 2005) and burning (Whelan 1995), whereas we found little effect (Fig. 1A). The lack of concordance between our results reported here, and those of earlier studies, likely results from our use of rarefaction methods to calculate richness and evenness. Rarefaction corrects for the greater likelihood of finding relatively rare species by chance alone at high-density sites, which inflates richness estimates and deflates evenness estimates (Alatalo 1981, Gotelli and Colwell 2001). Indeed, our raw data (i.e., without rarefaction) exhibit misleadingly strong benefits of organic agriculture and burning on richness, an underestimation of benefits for evenness, and a negative relationship between richness and evenness (Appendix B: Fig. B2). Thus, rarefaction techniques are instrumental to assessing the impacts of land-use management on biodiversity without being led astray by density-mediated sampling biases (e.g., Gotelli and Colwell 2001). Furthermore, our findings raise the intriguing possibility that any improvement in ecosystem function on organic farms and at burned sites that might otherwise have been attributed to gains in richness (Whelan 1995, Bengtsson et al. 2005, Hole et al. 2005), could instead result from increased evenness.

Further examination of the two sets of metadata allowed us to determine specifically how evenness was promoted. Relatively uncommon taxa experienced disproportionate density gains when shifting from conventional to organic agriculture or after burning was implemented in natural ecosystems (Fig. 1C). This meant that, while taxa at all points in the rank-abundance continuum generally gained individuals, relatively strong gains among rare taxa resulted in more equitable abundance distributions at organically farmed and burned sites. A similar pattern was seen when examining those taxa only detected under the high-density management regimes. These taxa joined organic and burned communities at densities roughly equal to the density gains exhibited by the rarest taxa found at both low- and high-density sites (Appendix B: Fig. B1). Thus, "new" taxa entered communities at relatively high relative abundances that did not strongly depress evenness scores. These same responses appeared to explain how evenness could change independent of richness: consistently strong gains in abundance among rare taxa increased evenness without requiring the addition of new taxa (Fig. 2A), while newly detected taxa generally conformed to existing relative-abundance distributions such that gains in richness did not necessarily alter overall evenness patterns (Fig. 2B). Thus, it was the general promotion of rare taxa that averted a richness–evenness trade-off.

We found little difference in richness between paired conventional and organic farms (Fig. 1A). One possible explanation for this similarity in richness is that fields of both types experienced "community saturation," reaching an intrinsic limit to richness even before management practices were changed (Elmendorf and Harrison 2011). Agroecosystems are managed to maximize plant productivity, and more productive environments are more likely to exhibit properties consistent with saturation such as strong interspecific competition, a positive relationship between richness and extinction rates, and a negative relationship between richness and colonization rates (Elmendorf and Harrison 2011). With little room to gain new species, any biodiversity benefit of organic farming

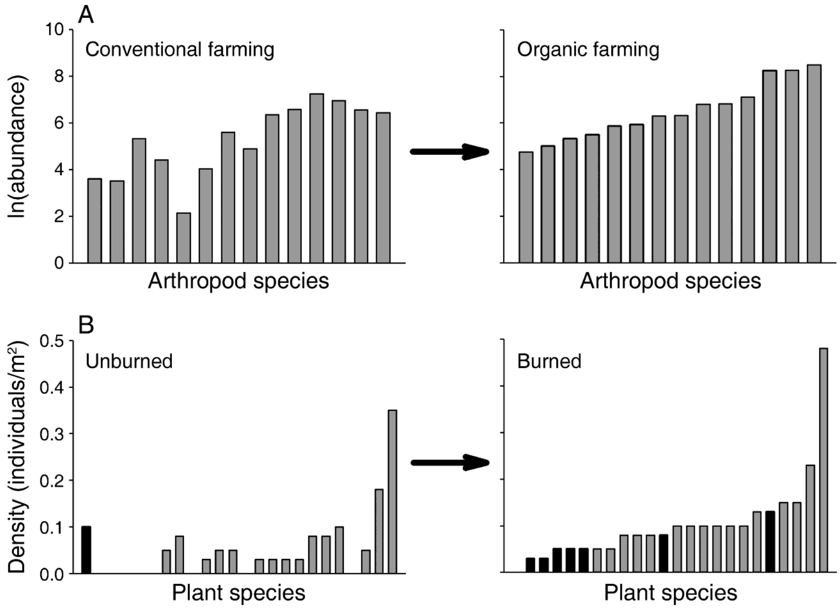

FIG. 2. Examples of the independent promotion of evenness or richness. Shown are typical studies that reflect the overall trends in the metadata sets. (A) Data from Ruano et al. (2004; see Appendix A and Supplement), where organic agriculture resulted in a 200% increase in abundance (number of individuals, here log-transformed) and a 32% increase in evenness in arthropod communities, with no change in richness. The increase in evenness results from greater similarity in abundance among species in the right-hand panel. (B) Data from Royo et al. (2010; see Appendix A and Supplement), where burning resulted in a 100% increase in abundance and a 50% increase in the number of plant species (species shown by gray bars are the same in both panels; species not found in one site are shown in black), but less than a 5% change in evenness. In both pairs of panels; the ordering of individual species is the same from left to right.

would have to result from a leveling of species' relative abundances, as we observed (Fig. 1A). Organic farming might benefit evenness through, for example, reduced use of pesticides harmful to sensitive species or increased use of animal-manure fertilizers that supplement detritus-based food webs (Maeder et al. 2002). In addition to its clear benefits for species balance, burning did promote a weak increase in species number that approached statistical significance (Fig. 1A). This suggests that burning might have created regeneration niches and/or removed competition from dominant plant species (Grubb 1977, Whelan 1995, Stohlgren et al. 2008), relaxing community saturation to allow species additions while also increasing densities of less abundant species already present. Thus, while organic agriculture and burning had remarkably similar overall effects on biodiversity, these effects might reflect different underlying mechanisms.

Greater evenness brings many benefits for ecosystem function that could be captured by organic farmers and those using fire for vegetation management. For example, more even communities of natural enemies provide more reliable herbivore suppression, while more even pollinator communities increase pollination efficiency, both to the benefit of plants (Ghazoul 2006, Tylianakis et al. 2007, Macfadyen et al. 2009, Crowder et al. 2010). More generally, consumers embedded within balanced communities can experience greater per capita foraging success due to reduced intraspecific competition, increasing community-wide resource extraction (Crowder et al. 2010). Greater evenness also benefits community resilience, for example, increasing the likelihood that bacterial communities can consistently perform denitrification in the face of salt stress (Wittebolle et al. 2009). Synergistic interactions among species also are more likely when species' relative abundances are similar than when broad abundance disparities are common (Hillebrand et al. 2008). Further work is needed to see if organic farms and burned sites do indeed realize these ecological benefits as resident species become more balanced.

We found that two common land-use management approaches promoted evenness with no concomitant benefit or harm to richness. That evenness could be conserved independent from any change in richness confirmed that these represent independent facets of biodiversity, but ran counter to the notion that richness and evenness would necessarily be expected to change in tandem or in opposition to one another. Nonetheless, somewhat paradoxically, evenness increased in response to the same general approach so effective throughout the long history of richness conservation: the selective promotion of rare taxa (Margules and Pressey 2000), albeit across a broader swath of the community. A key challenge for future research lies in unraveling the ecological processes that allow independent movement in evenness and richness, despite their often similar contributions to ecosystem function (Cardinale et al.

Plate 1. The adoption of organic farming practices in agricultural systems and controlled burns in natural plant communities are two common land-management schemes thought to benefit biodiversity. Shown are (A) an organic farm in Sandpoint, Idaho, USA, and (B) a controlled burn in the Kisatchie National Forest, Louisiana, USA. Photo credits: A, Joyce Parker; B, Matthew Ayres.

2006, Hillebrand et al. 2008). Experiments that separately manipulate richness from evenness, and vice versa, could provide a particularly powerful way to uncover the contribution of each biodiversity facet to ecosystem health and food-web interactions (e.g., Isbell et al. 2009, Wittebolle et al. 2009).

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Literature Cited

Alatalo, R. V. 1981. Problems in the measurement of evenness in ecology. Oikos 37:199–204.

Battisti, C., E. Ukmar, L. Luiselli, and M. A. Bologna. 2008. Diversity/dominance diagrams show that fire disrupts the evenness in Mediterranean pinewood forest bird assemblages. Community Ecology 9:107–113.

Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1125.

Bengtsson, J., J. Ahnström, and A.-C. Weibull. 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. Journal of Applied Ecology 42:261–269.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Chapin, F. S, III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lovorel, O. E. Sala, and S. E. Hobbie. M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature 405:234–242.

Crowder, D. W., T. D. Northfield, and W. E. Snyder. 2010. Organic farming promotes evenness and natural pest control. Nature 466:109–112.

De Benedictis, P. A. 1973. On the correlations between certain diversity indices. American Naturalist 107:295–302.

Elmendorf, S. C., and S. P. Harrison. 2011. Is plant community richness regulated over time? Contrasting results from experiments and long-term observations. Ecology 92:602–609.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94:295–304.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biology Reviews 52:107–145.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–1520.

Hole, D. G., A. J. Perkins, J. D. Wilson, I. H. Alexander, P. V. Grice, and A. D. Evans. 2005. Does organic farming benefit biodiversity? Biological Conservation 122:113–130.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586.

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

Jarvis, D. I., et al. 2008. A global perspective of the richness and evenness of traditional crop-variety diversity maintained by farming communities. Proceedings of the National Academy of Sciences USA 105:5326–5331.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Ma, M. 2005. Species richness vs. evenness: independent relationship and different responses to edaphic factors. Oikos 111:192–198.

Macfadyen, S., R. Gibson, A. Polaszek, R. J. Morris, P. G. Craze, R. Planque, W. O. C. Symondson, and J. Memmott. 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? Ecology Letters 12:229–238.

Maeder, P., A. Fliessbach, D. Dubois, L. Gunst, P. Fried, and U. Niggli. 2002. Soil fertility and biodiversity in organic farming. Science 296:1694–1697.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

May, R. M. 1975. Patterns of species abundance and diversity. Pages 81–120 *in* M. L. Cody and J. L. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, USA.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperature forest herbaceous diversity. Ecology 91:93–105.

Ruano, F., C. Lozano, P. Garcia, A. Pena, A. Tinaut, F. Pascual, and M. Campos. 2004. Use of arthropods for the evaluation of the olive-orchard management regimes. Agricultural and Forest Entomology 6:111–120.

SAS Institute. 2009. JMP version 9.0. SAS Institute, Cary, North Carolina, USA.

Shafi, M. I., and G. A. Yarranton. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. Ecology 54:897–902.

Smith, B., and J. T. Wilson. 1996. A consumer's guide to evenness indices. Oikos 76:70–82.

Soininen, J., S. Passy, and H. Hillebrand. 2012. The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. Oecologia. http://dx.doi.org/10.1007/s00442-011-2236-1

Srivastava, D. S., and M. Vellend. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? Annual Review of Ecology Evolution and Systematics 36:267–294.

Stirling, G., and B. Wilsey. 2001. Empirical relationships between species richness, evenness, and proportional diversity. American Naturalist 158:286–299.

Stohlgren, T. J., D. T. Barnett, C. S. Jarnevich, C. Flather, and J. Kartesz. 2008. The myth of plant species saturation. Ecology Letters 11:313–322.

Svensson, J. R., M. Lindegarth, P. R. Jonsson, and H. Pavia. 2012. Disturbance-diversity models: what do they really predict and how are they tested? Proceedings of the Royal Society of London B 279:2163–2170.

Tylianakis, J. M., T. Tscharntke, and O. T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445:202–205.

Whelan, R. J. 1995. The ecology of fire. Cambridge University Press, New York, New York, USA.

Wilsey, B. J., D. R. Chalcraft, C. M. Bowles, and M. R. Willig. 2005. Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. Ecology 86:1178–1184.

Wittebolle, L., M. Marzorati, L. Clement, A. Balloi, D. Daffonchoi, K. Heylen, P. De Vos, W. Verstraete, and N. Boon. 2009. Initial community evenness favours functionality under selective stress. Nature 458:623–626.

Supplemental Material

Appendix A

Reference list for studies in the metadata sets (*Ecological Archives* E093-190-A1).

Appendix B

Methods related to the choice of evenness indices and data analyses, two tables containing results of the mixed-effect models, and two figures showing results from the meta-analysis (*Ecological Archives* E093-190-A2).

Supplement

Information on the studies in the metadata sets and the Visual Basic code associated with the rarefactions (*Ecological Archives* E093-190-S1).