

Biodiversity and tallgrass prairie decomposition: the relative importance of species identity, evenness, richness, and micro-topography

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Received: 27 July 2008 / Accepted: 19 December 2008 / Published online: 13 January 2009
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Abstract Biodiversity has been declining in many areas, and there is great interest in determining whether this decline affects ecosystem functioning. Most biodiversity—ecosystem functioning studies have focused on the effects of species richness on net primary productivity. However, biodiversity encompasses both species richness and evenness, ecosystem functioning includes other important processes such as decomposition, and the effects of richness on ecosystem functioning may change at different levels of evenness. Here, we present two experiments on the effects of litter species evenness and richness on litter decomposition. In the first experiment, we varied the species evenness (three levels), identity of the dominant species (three species), and micro-topographic position (low points [gilgais] or high points between gilgais) of litter in three-species mixtures in a prairie in Texas, USA. In a second experiment, we varied the species evenness (three levels), richness (one, two, or four species per bag), and composition (random draws) of litter in a prairie in Iowa, USA. Greater species evenness significantly increased decomposition, but this effect was dependent on the environmental context. Higher

evenness increased decomposition rates only under conditions of higher water availability (in gilgais in the first experiment) or during the earliest stages of decomposition (second experiment). Species richness had no significant effect on decomposition, nor did it interact with evenness. Micro-topographic position and species identity and composition had larger effects on decomposition than species evenness. These results suggest that the effects of litter species diversity on decomposition are more likely to be manifested through the evenness component of diversity than the richness component, and that diversity effects are likely to be environmentally context dependent.

Keywords Ecosystem functioning · Litter bag · Litter quality · Grassland · Moisture · Time

Introduction

Biodiversity has been declining in many areas due to habitat loss (Rosenzweig 1995), eutrophication (Tilman 1987), and human management practices (Engle et al. 1993). The effect of declining species diversity on ecosystem process rates (ecosystem functioning, EF) is of both theoretical and applied interest (Loreau et al. 2002). Most studies of biodiversity—EF have focused on primary productivity because of its obvious importance to ecosystems (Loreau et al. 2002). However, both decomposition and primary

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productivity control nutrient and energy flow. The rate of return of nutrients from decomposing plant tissue can limit primary productivity in the long run, and litter forms the basis for the detritivore food web, which contains more energy than the herbivore food web in most ecosystems (Swift et al. 1979). Furthermore, a full understanding of decomposition processes is important in predicting carbon sequestration rates and feedbacks that impact global warming (Swift 2001). Thus, it is important to develop a better understanding of how decomposition is affected by changes in litter diversity.

Biodiversity encompasses both species richness and evenness (Magurran 1988). Different components of biodiversity such as beta diversity can also encompass the change in species composition over space. However, in this study we focus on alpha diversity by varying litter diversity at individual points. Early studies of biodiversity and EF emphasized the species richness component of biodiversity (Loreau et al. 2002), but more recent studies have examined the effects of both species richness and evenness on EF (Nijs and Roy 2000; Mulder et al. 2004; Wilsey and Polley 2004; Emery and Gross 2006; Boyero et al. 2007; Kirwan et al. 2007; McKie et al. 2008; Swan et al. accepted). In studies focusing on the effects of species richness on EF, all species were generally added at the same relative proportions (i.e., at maximum evenness), whereas natural systems typically have low evenness (Preston 1962; Tokeshi 1993; Schwartz et al. 2000; Wilsey et al. 2005). A literature survey found that plant species evenness accounted for 53% of variation in plant species diversity (Shannon's H'), while plant species richness accounted for only 6% of the variation across community types (with covariation between evenness and richness accounting for the remaining variation; Stirling and Wilsey 2001). Thus, studies which do not take into account species evenness do not examine the full effects of changes in diversity because they do not encompass both components of biodiversity.

The applicability of species richness—EF studies has also been questioned by researchers, who suggested that the apparent effects of high species richness were actually due to the greater likelihood of including particular species that strongly affect EF (the “sampling effect”; Aarssen 1997; Huston 1997; Tilman et al. 1997). The sampling effect could

underlie some of the effects of litter species richness in studies of decomposition (Hector et al. 2000; Knops et al. 2001), although it is important to emphasize that Tilman et al. (2001) found transgressive overyielding effects of species richness that go beyond the sampling effect. In contrast, the effects of species evenness cannot be attributed to the sampling effect, since the identity of species does not change at different evenness levels, only the relative abundance of species (Wilsey and Potvin 2000; Loreau et al. 2001; King et al. 2002). Thus, by varying species diversity through changes in evenness, we are able to test for diversity effects in the absence of the sampling effect (Wilsey and Potvin 2000; Loreau et al. 2001; King et al. 2002).

Species evenness could commonly interact with richness to affect EF (Doak et al. 1998; Schwartz et al. 2000; Dangles and Malmqvist 2004; Swan et al. accepted). In sites with low evenness, one or more dominant species could have strong effects on EF and the remaining rare species could have a negligible effect on EF (e.g., Smith and Knapp 2003). However, in sites with high evenness, each species has a similar abundance and the addition or removal of a species may have appreciable effects on EF. If the effect of species richness depends on evenness, then this interaction would need to be fully understood before making inferences from richness-EF studies to field situations (Schwartz et al. 2000; Srivastava and Vellend 2005).

The two previous studies on the effects of litter species evenness on decomposition found mixed results. King et al. (2002) found no effects of litter evenness on litter decomposition in laboratory microcosms. Swan et al. (accepted) found that litter evenness and richness interacted to significantly affect leaf litter decomposition in a stream. The highest decomposition rates were found when evenness was closer to field values.

Plant species diversity could affect litter decomposition through mechanisms involved with litter mixing. The chemical environment and decomposer community changes when litter is mixed as long as species differ in resource quality or structure (Blair et al. 1990; Smith and Bradford 2003; Gartner and Cardon 2004). By mixing species at different litter evenness levels, the ratios of different types of phenolics, textures, and nutrients in the mixture are altered. Evenness could affect decomposition rates

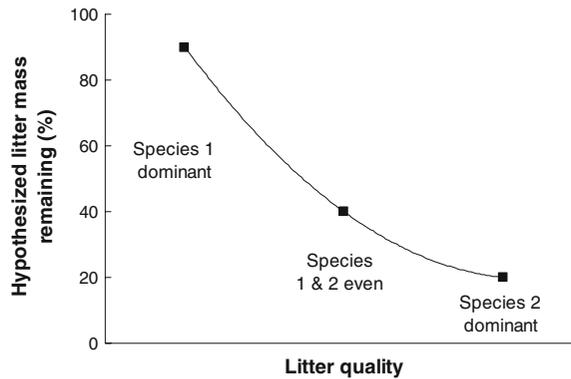


Fig. 1 Hypothesized relationship between decomposition rate and litter mixes at different levels of litter species evenness. If the litter decomposition rate is non-linearly related to litter quality then mixing litter at high evenness could increase mean

due to non-linear responses of decomposition to changes in stoichiometry and litter quality (Fig. 1; Melillo et al. 1982).

Decomposition is strongly affected by factors other than biodiversity, and therefore, the effects of biodiversity must be studied in the context of abiotic and other biotic variables. Rates of litter decomposition can vary with soil moisture (Zhang and Zak 1995; Walse et al. 1998), temperature (Hobbie 1996), and microbial community composition (Chapela and Boddy 1988; Zhang and Zak 1995). Abiotic and biotic variables not related to biodiversity can sometimes have a greater direct effect on decomposition than biodiversity (Wardle et al. 1997b), and could interact with biodiversity.

We tested the general hypothesis that decreases in litter species diversity will cause declines in litter decomposition. In two separate experiments, we manipulated species evenness and species identity or composition in litter bags. We also manipulated species richness in one experiment and micro-topographic location (i.e., in a soil depression [gilgai] or not) in the other experiment. We used these experiments to test the following predictions: (1) higher litter species evenness will cause an increase in litter decomposition; (2) evenness will interact with micro-topographic factors such that the effect of evenness on litter decomposition will be larger at lower topography, where soil moisture is higher; and (3) effects of species richness on litter decomposition will be smaller in the presence of realistically low levels of litter evenness.

decomposition rates. In this example, low evenness bags would have a hypothetical mean remaining biomass of $(90\% + 20\%)/2 = 55\%$, whereas high evenness bags would have a mean of 40%

Methods

Clymer Prairie experiment

The Clymer Meadow Prairie Preserve is located in the blackland prairie region of northeast Texas, USA near the town of Greenville. The preserve encompasses several hundred hectares and is owned by The Nature Conservancy. Soils are vertisols, and the dominant vegetation at the site is represented by tallgrass prairie species (Polley et al. 2005). Mean annual precipitation is 111 cm, and average monthly precipitation shows a bimodal distribution with peaks in May (14 cm) and October (12 cm) and a minimum in August (6 cm). Daily average temperatures range from a low of 0°C in January to a high of 34°C in July and August (Greenville weather station).

In August 2000, leaves of three common species (the forb *Helianthus maximiliani*, and the C₄ grasses *Schizachyrium scoparium*, and *Sporobolus compositus*) were collected and placed in litter bags (all Texas taxonomy follows Diggs et al. 1999). Litter bags were made from 12 × 30 cm polypropylene fabric with openings of 0.25 × 0.5 mm, which is the same material used in a multiple-site study across Canada (Moore et al. 1999). A litter species richness of three was used for all litter bags in this experiment because that is typical of the number of species that would be found at the very small scale of the litter bag. All bags contained 6 g of leaf litter. Litter evenness, dominant species identity, and placement of bags varied in a 3 × 3 × 2 factorial treatment arrangement, with three

species evenness treatments, three dominant species identity treatments, and two micro-topographic location treatments. Litter species evenness treatments were applied by varying the proportion of the dominant species, such that high evenness had 3 g of the dominant species and 1.5 g of the other two species, medium evenness had 4 g of the dominant species and 1 g of the other two, and low evenness had 5 g of the dominant species and 0.5 of the other two. The identity of the dominant species was either *H. maximiliani*, *S. scoparium*, or *S. compositus*. These proportions of species correspond to Simpson's evenness levels of 0.89, 0.67, and 0.47 from high to low evenness, which is somewhat higher than the Simpson's evenness calculated from the plant biomass of moderately sized plots (0.71 × 0.71 m) from nearby Texas prairie remnants and restorations (range of evenness 0.08–0.30; Polley et al. 2005). The micro-topographic treatment was either in a gilgai or between gilgais (a gilgai is a seasonally wet depression created by soil expansion and contraction due to soil cracking in dry weather; Edelman and Brinkman 1962; Russell and Moore 1972). In our system, gilgais created large differences in moisture availability and elevation, and these differences greatly affected plant species composition, with more mesic species within gilgais and more xeric species between gilgais (B. Wilsey, personal observations).

Litter bags were placed on the soil surface in September 2000. All bags were placed in random locations so that all treatments (litter evenness, dominant species, micro-topography, and time) were fully interspersed. There were five collection periods (3 weeks; 6 weeks; 12 weeks; 24 weeks; and 48 weeks after September 2000), and each of the treatments was replicated twice within each collection period, leading to 180 litter bags in total (3 litter evenness levels × 3 dominant species × 2 micro-topographic treatments × 5 collection periods × 2 replicates). Thus, there was low replication for the higher order interactions, but high replication of the main effects ($n = 60$ for each litter evenness and species identity level, and $n = 90$ for each micro-topographic treatment) and one-way interactions (e.g., $n = 20$ for each litter evenness × gilgai combination) due to hidden replication inherent in factorial designs (Steel and Torrie 1980).

We estimated the carbon (C) to nitrogen (N) mass ratio from litter shortly after it was collected (time zero). We analyzed three replicates of each of the

three species used. Litter C and N was estimated by grinding samples through a Wiley mill and then running samples through a CE Elantech flash EA 1112 combustion C:N analyzer.

Doolittle Prairie experiment

The Doolittle Prairie is a tallgrass prairie in the state preserve system located near Ames, Iowa, USA in the central portion of the state. Soils are mollisols, and vegetation is a highly diverse mix of grasses and forbs (described by Wetzel et al. 1999). Mean annual precipitation is 87 cm, and average monthly precipitation shows a unimodal distribution with a peak in June (13 cm) and a minimum in January (2 cm). Daily average temperatures range from a low of -13°C in January to a high of 29°C in July (Ames weather station).

In late October 2001, leaves of eleven common species were collected from Doolittle and other local prairies (C_4 grasses *Andropogon gerardii*, *Sorghastrum nutans*, *Panicum virgatum*, *Schizachyrium scoparium* and *Sporobolus compositus*, the C_3 grass *Elymus canadensis*, and the forbs *Ratibida pinnata*, *Eryngium yuccifolium*, *Silphium laciniatum*, *Solidago canadensis*, and *Solidago rigida*; all Iowa taxonomy except *S. compositus* follows Eilers and Roosa 1994). Litter bags were made from the same material as the Clymer Prairie experiment: 12 × 30 cm polypropylene fabric with openings of 0.25 × 0.5 mm (Moore et al. 1999), and again, all bags contained 6 g of leaf litter. Mixture bags were established with 2 × 3 factorial treatment arrangement that varied litter species richness (two or four species), and litter species evenness (high, medium, and low denoted by $k = 0$; $k = 2$; $k = 4$, respectively). The chosen values of litter species evenness encompassed the values calculated from the plant biomass of moderately sized plots (0.4 × 1.0 m) from nearby Iowa prairie remnants and restorations (range of k 1.4 to 2.6; Losure et al. 2007). Richness levels were at the lower end of the number of plant species rooted within 12.5 × 12.5 cm plots at Doolittle Prairie (range 2–12; Yurkonis Unpubl.). Richness levels were established by randomly drawing either two or four species from the 11 species pool, with four random draws per richness level. Evenness was varied by changing the slope of rank-abundance relationships as outlined by Wilsey and

Polley (2004). Litter mass of each species was varied so that species rank-abundance curves become more negative as k increases in a geometric series model (Tokeshi 1993). For example, a four-species mixture including *S. nutans*, *S. laciniatum*, *E. canadensis*, and *S. rigida* with $k = 4$ contained 4.52 g *S. nutans*, 1.13 g *S. laciniatum* (i.e., 4.52 g/4), 0.28 g *E. canadensis* (1.13 g/4), and 0.07 g *S. rigida* (0.28 g/4), whereas a four species mixture with $k = 0$ contained 1.5 g for all four species. Given a particular value of k , the slopes of rank-abundance curves stay the same across litter richness treatments, thereby allowing a test of the richness \times evenness interaction (Wilsey and Polley 2004). Each of the 11 species used was also placed in single-species monoculture bags.

Litter bags were placed on the soil surface in March 2002 within two areas (blocks). Blocks were established by aligning litter bags along a compass line. All bags were placed in random locations within blocks so that all treatments (litter evenness, litter richness, and time) were fully interspersed. There were three collection periods (4 weeks, 8 weeks, and 32 weeks), and each of the treatments was applied to two blocks within each collection period, leading to 144 mixture bags in total (4 random species draws \times 2 litter richness levels \times 3 litter evenness levels \times 3 collection periods \times 2 blocks), and 66 monoculture bags in total (11 species \times 3 collection periods \times 2 blocks).

Statistical methods

All analyses were completed with SAS 8.0 using type III sum of squares to account for unequal sample sizes (a few litter bags were lost in the field). Proc GLM was used for the Clymer Prairie analysis, with all variables entered as fixed effects in a fully factorial analysis. Proc Mixed was used for the Doolittle Prairie analysis, with species draw as a random factor nested within litter richness levels (two and four species). All other factors were fixed. We included time as a fixed factorial factor because we specifically chose the timing of each collection period and because litter bag location was random across collection periods (i.e., time was not a nested treatment). When interactions with litter evenness occurred, we performed linear and quadratic contrast statements in SAS to test whether evenness affected litter decomposition in a linear or quadratic manner at different levels of the interacting variable (ex. gilgai

at Clymer and time at Doolittle; Littell et al. 2002). The x -axis values for the contrasts were Simpson's evenness levels in the Clymer experiment (0.89, 0.67, 0.47 from high to low evenness), and rank-abundance slopes in the Doolittle experiment (0, 2, 4 from high to low evenness; Wilsey and Potvin 2000; Wilsey and Polley 2004). C:N ratios in the Clymer experiment were analyzed with a non-parametric Kruskal–Wallis analysis due to heterogeneity of variances.

We could not use monocultures in a factorial analysis including evenness because the evenness of monocultures cannot be varied. To test the effects of richness in the Doolittle Prairie while including monocultures, we performed the same analysis as above, except we included monocultures and did not test for evenness effects. This analysis separated effects of species composition from effects of litter species richness by including the effects of species draws at all richness levels.

Results

Clymer Prairie experiment

Litter mass decreased 46.7% on average over the 48 weeks of the experiment. Decomposition over time varied between dominant species and gilgai treatments, with effects of dominant species identity and gilgai becoming more pronounced over time (significant time \times species identity \times gilgai interaction; Table 1; Fig. 2). Litter mass decreased the fastest when *Helianthus maximiliani* was dominant within gilgais, decreased moderately when *Sporobolus compositus* was dominant, and decreased the slowest when *Schizachyrium scoparium* was dominant outside gilgais (Fig. 2). Greater decomposition was found in species with lower initial C:N ratios since *H. maximiliani* had the lowest initial C:N ratio (mean 40.9, standard error 0.3) followed by *S. compositus* (mean 51.8, standard error 1.3) and *S. scoparium* (mean 76.9, standard error 6.5; the C:N ratios were significantly different; χ^2 with 2 d. f. = 7.2, $P = 0.027$).

Although species identity and gilgai had the largest effects on litter decomposition, we also found effects of species evenness. The effects of evenness were variable depending on whether litter bags were placed within gilgais or between gilgais (significant evenness \times gilgai interaction; Table 1; Fig. 3). Litter

Table 1 ANOVA results for observed remaining litter mass at Clymer Prairie, Texas

Predictor variable	d. f.	Sum of Squares	F-values	P-values
Evenness	2	0.52	4.21	0.019
Dominant species identity	2	6.08	48.77	<0.001
Gilgai	1	0.59	9.41	0.003
Evenness × dominant species ID	4	0.24	0.97	0.431
Evenness × gilgai	2	0.67	5.36	0.007
Dominant species ID × gilgai	2	0.52	4.20	0.019
Evenness × dominant species ID × gilgai	4	0.29	1.17	0.329
Time	4	111.09	445.80	<0.001
Time × evenness	8	0.42	0.84	0.574
Time × dominant species ID	8	1.32	2.65	0.013
Time × gilgai	4	1.31	5.27	<0.001
Time × evenness × dominant species ID	16	1.41	1.41	0.158
Time × evenness × gilgai	8	0.45	0.89	0.526
Time × dominant species ID × gilgai	8	1.06	2.13	0.043
Time × evenness × dominant species ID × gilgai	16	0.91	0.91	0.563
Residual	77	4.80		

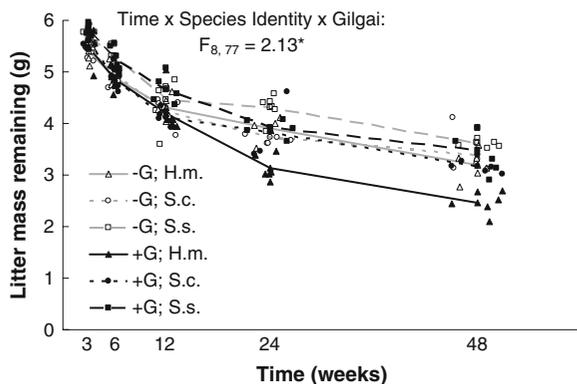


Fig. 2 Amount of litter mass remaining in different treatments at Clymer Prairie, Texas (* $P < 0.05$; G = gilgai; H.m. = *Helianthus maximiliani*; S.c. = *Sporobolus compositus*; S.s. = *Schizachyrium scoparium*; data points are jiggered on the x-axis)

evenness had no significant effect on decomposition outside gilgais (linear and quadratic contrasts $P > 0.1$), but higher evenness caused a 5.7% saturating decline in litter mass inside gilgais (linear contrast $F_{1,77} = 15.5$, $P < 0.001$; quadratic contrast $F_{1,76} = 3.21$, $P = 0.077$).

Doolittle Prairie experiment

Litter mass decreased 26.4% on average over the 32 weeks of the experiment. Similar to the Clymer

Prairie study, we found large effects of species composition (random species draws) at all time periods (Table 2).

Litter evenness affected decomposition primarily during the early part of the experiment (significant time × evenness interaction; Table 2; Fig. 4). There were opposite quadratic relationships between evenness and decomposition after 4 weeks (5.5% decrease in litter mass from moderate to high evenness; $F_{1,105} = 6.60$, $P = 0.012$) and 32 weeks (4.6% increase in litter mass from moderate to high evenness; $F_{1,105} = 4.99$, $P = 0.028$), and no other significant linear or quadratic relationships ($P > 0.1$). An extreme data point (3.47 g litter mass remaining) at 32 weeks moderate litter evenness had a large impact on the quadratic relationship at this time ($F_{1,104} = 2.97$, $P = 0.088$ when data point was removed), but had little impact on the overall time × evenness interaction ($F_{4,103} = 3.08$, $P = 0.019$ when data point was removed). Importantly, evenness did not interact with richness ($P > 0.1$) and there were no significant differences in decomposition between litter bags containing two and four species ($P > 0.1$). Richness also had no significant effects on decomposition when including monocultures in the analysis (i.e., between litter bags containing one, two, and four species; $P > 0.1$).

Fig. 3 The effects of litter species evenness on average litter mass across time periods at Clymer Prairie, Texas both outside and inside gilgais (** $P < 0.01$). All error bars are +1 standard error

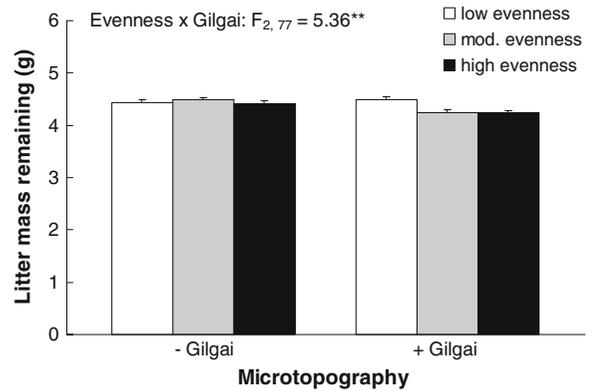


Table 2 ANOVA results for observed remaining litter mass at Doolittle Prairie, Iowa

Predictor ^a variable	d. f.	Sum of squares	F-values	P-values
Block	1	0.08	1.02	0.315
Richness ^b	1	1.48	1.97	0.210
Species draw(richness) ^c	6	4.53	17.05	<0.001
Evenness	2	0.20	1.24	0.294
Richness × evenness	2	0.23	1.44	0.241
Time ^c	2	19.73	222.37	<0.001
Time × richness ^c	2	0.01	0.10	0.905
Time × species draw	12	0.53	0.55	0.878
Time × evenness	4	1.11	3.43	0.011
Time × richness × evenness	4	0.22	0.69	0.600
Residual	104	8.38		

^a F-values are determined by dividing the mean square value for each variable by the residual mean square value unless otherwise noted

^b F-value is determined by dividing the mean square value of this variable by the mean square value of species draw

^c F-value is determined by dividing the mean square value of this variable by the mean square value of time × species draw

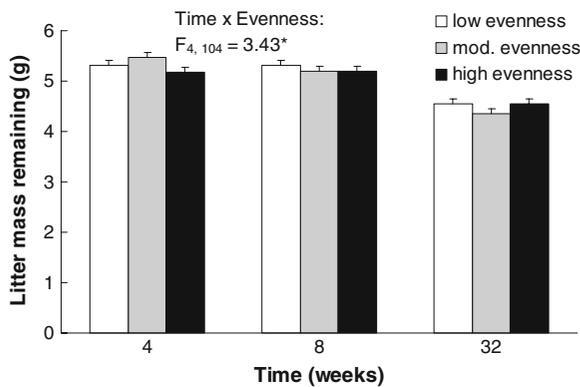


Fig. 4 The effects of litter species evenness on litter mass at Doolittle Prairie, Iowa after 4, 8, and 32 weeks (* $P < 0.05$). Error bars are +1 standard error

Discussion

Our experiments tested the general hypothesis that both components of litter species diversity, species evenness and richness, would affect litter decomposition individually and interactively, respectively. Our first prediction was that higher species evenness would cause an increase in litter decomposition. This prediction received some support, although evenness effects were dependent on the environmental context. In support of our second prediction, higher litter evenness caused the greatest decomposition, when litter bags were placed inside gilgais (soil depressions) in the Clymer experiment. Our third prediction was that the effects of litter species richness on decomposition would be smaller at realistically low levels of

litter species evenness. This prediction was not supported. Similar to Knops et al. (2001) and Wardle et al. (1997a), we found no significant effects of litter richness on decomposition, and richness did not interact with litter evenness to affect decomposition. The absence of a richness effect was not likely due to problems with statistical power. Our experimental design was able to detect relatively small differences (<10%) in litter mass, which suggests that we had sufficient statistical power with our design. Finally, the effects of biodiversity on ecosystem functioning (EF) appear to be more strongly dependent on environmental conditions than species diversity.

Other studies have also found that biodiversity is not the primary determinant of EF. Hooper and Vitousek (1997) first noted that plant species richness effects on productivity are smaller than species identity effects. Wardle et al. (1997b) found that fire frequency and species identity had larger effects than plant richness on single-species litter decomposition, standing-crop biomass, and nitrogen mineralization across islands. Walse et al. (1998) found that increased moisture availability led to higher rates of decomposition, which is consistent with our finding of higher decomposition within gilgais. It is interesting to note, however, that even though topography strongly affected decomposition on its own, it strongly interacted with evenness as well. Therefore, the effects of species evenness on EF must be considered within the context of abiotic effects.

We are aware of only two other studies that deal with the effect of plant species evenness on litter decomposition. Swan et al. (accepted) found an effect of litter species evenness on decomposition, but, unlike our study, this effect varied at different litter richness levels. In contrast to our experiments, King et al. (2002) found no effects of woody species leaf litter evenness on litter decomposition, microbial respiration, dissolved organic carbon, or inorganic nitrogen release. However, the King et al. (2002) study was completed in a laboratory with little environmental variability. Higher evenness may lead to greater decomposition in mixtures in variable environments but may have little effect when the environment is stable. This notion is supported by litter evenness effects appearing in the more variable wet–dry environment found within gilgais but not in the more consistent environment outside gilgais. Gilgais contained standing water during January

(mean 67 mm, range 42–97) and March (mean 53 mm, range 27–77) of the growing season but did not contain standing water from April until the following winter. Between gilgais it was more consistently dry.

The interaction between evenness and time in the Doolittle experiment may have been due to the different litter fractions (labile and recalcitrant) that exist over time or the differing importance of bacterial versus fungal decomposition through time. For example, phenolic compounds make up a greater percentage of remaining litter weight over time (Minderman 1968), and evenness may affect litter decomposition differently across time if decomposition is limited by nutrients in the early stages and phenolics in the later stages (Berg and Staaf 1980). It has also been shown that bacteria and fungi are more effective at decomposing different fractions of litter material (Benner et al. 1984), which creates a situation where bacteria and fungi differ in their relative rates of decomposition at different times (Aumen 1980; Ingham et al. 1985). Although not studied here, we hypothesize that the differing effects of litter evenness over time in the Doolittle experiment could potentially be explained by evenness affecting the decomposition of different fractions of litter material differently, by evenness affecting bacterial and fungal communities differently, or both. Future studies should examine the potential mechanisms by which the effects of evenness may change over time.

Several authors have hypothesized that the relationship between species richness and EF would change at different levels of evenness (Doak et al. 1998; Schwartz et al. 2000). A reduced richness effect at realistically low levels of evenness could reduce the applicability of many species richness—EF studies since these studies are generally designed for maximal evenness, whereas most natural communities have much lower evenness (Preston 1962; Loreau et al. 2002; although Hooper and Dukes 2004 showed maximal evenness can sometimes decline to more natural levels over time). Dangles and Malmqvist (2004) found that the effects of detritivore species richness can change across different levels of detritivore evenness, and Swan et al. (accepted) found that litter richness and evenness interacted to affect decomposition of leaves in a stream. Our study is the first to test whether an interaction exists between litter

species richness and evenness on terrestrial plant decomposition, and because we found no interaction, the effects of litter species richness on decomposition in past terrestrial studies (Loreau et al. 2002) may not change qualitatively at different evenness levels, even though further tests are needed.

Our results suggest that the effects of litter species diversity on decomposition are more likely to be manifested through the evenness component of diversity than the richness component, and that diversity effects are likely to be environmentally context dependent. Past studies of the effects of plant litter richness on decomposition have found little to no effect of richness on decomposition (Wardle et al. 1997a; Hector et al. 2000; Knops et al. 2001). Our study and another study (Swan et al. accepted) suggest that changes in litter evenness can affect litter decomposition. Therefore, the evenness component of biodiversity is important in understanding the effects of biodiversity on decomposition. Most studies have shown that increased plant species richness can increase net primary productivity (Loreau et al. 2002). Large standing litter pools could develop if increased richness causes an increase in primary productivity without an accompanying increase in decomposition. These litter pools could eventually have negative feedback effects on productivity in environments without disturbance (Knops et al. 2001). In contrast, the effects of plant species evenness on productivity were not consistent between studies (reviewed by Hillebrand et al. 2008). However, higher evenness may increase productivity and nutrient availability over time by increasing decomposition rates and decreasing standing litter pools, at least in some environments.

Acknowledgments We thank Megan Davenport, Brad Bauer, and Dan Haug for help with sample processing. Anna Loan-Wilsey helped us to collect litter. Philip Dixon consulted with us on statistical analyses.

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