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IS PHYLOGENETIC AND FUNCTIONAL TRAIT DIVERSITY A DRIVER OR CONSEQUENCE OF GRASSLAND COMMUNITY ASSEMBLY?

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Resource addition drives taxonomic divergence and phylogenetic convergence of plant communities

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Abstract

1. Anthropogenic environmental changes are known to affect the Earth's ecosystems. However, how these changes influence assembly trajectories of the impacted communities remains a largely open question.
2. In this study, we investigated the effect of elevated nitrogen (N) deposition and increased precipitation on plant taxonomic and phylogenetic β-diversity in a 9-year field experiment in the temperate semi-arid steppe of Inner Mongolia, China.
3. We found that both N and water addition significantly increased taxonomic β-diversity, whereas N, not water, addition significantly increased phylogenetic β-diversity. After the differences in local species diversity were controlled using null models, the standard effect size of taxonomic β-diversity still increased with both N and water addition, whereas water, not N, addition, significantly reduced the standard effect size of phylogenetic β-diversity. The increased phylogenetic convergence observed in the water addition treatment was associated with colonizing species in each water addition plot being more closely related to species in other replicate plots of the same treatment. Species colonization in this treatment was found to be trait-based, with leaf nitrogen concentration being the key functional trait.
4. *Synthesis*. Our analyses demonstrate that anthropogenic environmental changes may affect the assembly trajectories of plant communities at both taxonomic and phylogenetic scales. Our results also suggest that while stochastic processes may cause communities to diverge in species composition, deterministic process could still drive communities to converge in phylogenetic community structure.

KEYWORDS

community assembly, global change ecology, nitrogen fertilization, phylogenetic β-diversity, precipitation change, semi-arid steppe, taxonomic β-diversity

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1 | INTRODUCTION

Understanding mechanisms driving compositional variation across ecological communities, frequently referred to as β-diversity, is one of the major goals of community ecology (Anderson et al., 2011; Chase & Myers, 2011; Whittaker, 1960). Across large spatial scales, evolutionary and biogeographic processes such as in situ diversification may constitute an important source of β-diversity (Graham & Fine, 2008; Ricklefs, 2006, 2008). Ecological theories that explain β-diversity among communities, which generally ignore evolutionary processes, fall into two broad categories. The niche theory suggests that β-diversity arises largely from deterministic processes, driven by ecological selection favouring different species across localities characterized by different environmental conditions (Chase & Leibold, 2003). In contrast, the neutral theory suggests that β-diversity could simply arise from ecological drift, driven by stochastic processes such as chance colonization and random demographic events (Bell, 2001; Hubbell, 2001). Ecological communities are known to be subject to the influence of both niche-based ecological selection, which would cause communities sharing similar environmental conditions to be structurally similar (i.e. low β-diversity), and stochasticity-based ecological drift, which could cause substantial structural dissimilarity among communities (i.e. high β-diversity) even in similar environments (Adler, HilleRisLambers, & Levine, 2007; Gravel, Canham, Beaudet, & Messier, 2006; Leibold & McPeek, 2006). As anthropogenic environmental changes, such as increased nitrogen (N) deposition and changing precipitation, continue to affect ecosystems world-wide (Vitousek, Mooney, Lubchenco, & Melillo, 1997), it is essential to understand how these changes affect the relative importance of the two contrasting processes in shaping community assembly, and, consequently, β-diversity among the assembled communities.

Anthropogenic environmental changes in the form of resource amendment (e.g. increased N deposition and elevated precipitation) may have the potential to impact the trajectory of community assembly, and thus β-diversity in opposite directions. For example in environments where limited resource supply presents an important environmental filter that excludes many species whose resource requirements are not met, increased resource input may relieve environmental harshness and allow a greater number of species to successfully colonize the habitat; the resulting larger species pool could then more readily give rise to alternative community states (Chase, 2003; Fukami, 2004; Jiang, Joshi, Flakes, & Jung, 2011; Law & Morton, 1993; Levine, Bascompte, Adler, & Allesina, 2017; Saavedra et al., 2017), resulting in increased β-diversity. The increased environmental productivity under resource enrichment may further promote the presence of alternative community states (Chase, 2010; Ejrnæs, Bruun, & Graae, 2006; Isbell, Tilman, Polasky, Binder, & Hawthorne, 2013). On the other hand, increased resource input may favour species with certain traits but make the condition less favourable for other species (e.g. Dickson, Mittelbach, Reynolds, & Gross, 2014), which would lead to increased dominance of the same species assemblages across communities, resulting in reduced β-diversity. In addition, resource enrichment may often cause the reduced availability of other resources and increased intensity of competition for these resources (e.g. light for plants, Hautier, Niklaus, & Hector, 2009), accelerating deterministic competitive exclusion.

Notably, existing studies on the response of β-diversity to environmental changes have focused on taxonomic β-diversity that captures turnover in species composition among sites (Chase, 2007, 2010; Myers, Chase, Crandall, & Jiménez, 2015; Zhang, Liu, Bai, Zhang, & Han, 2011). It is less clear how phylogenetic β-diversity, which accounts for evolutionary relationships among species, responds to environmental changes [but see Guo et al. (2018) for a study of climate warming on soil microbial communities]. Studying phylogenetic β-diversity, however, could provide novel insight into how communities respond to environmental changes beyond those obtained via studying taxonomic β-diversity alone (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Graham & Fine, 2008; Hardy, Couteron, Munoz, Ramesh, & Pélissier, 2012). For instance the study of both taxonomic and phylogenetic β-diversity could allow the exploration of the idea that the degree of determinism in community assembly may depend on the level of ecological organization examined (Diamond, 1975; Fox, 1987; Fukami, Bezemer, Mortimer, & Putten, 2005). A group of phylogenetically closely related species may exhibit largely similar responses to environmental changes, by virtue of their similar traits, making the group-level response more deterministic. However, changes in individual species within the group may be less deterministic, as the result of ecological drift influencing populations of closely related species. We thus hypothesize that taxonomic and phylogenetic β-diversity may not necessarily show similar responses to environmental changes.

Changes in species taxonomic and phylogenetic β-diversity may be better understood by looking into species extinction and colonization patterns. Species loss may depend on their traits and evolutionary history, such that species of certain clades may suffer greater extinction risk than species of other clades (Purvis, Agapow, Gittleman, & Mace, 2000). For example legumes, which can well tolerate low soil N concentrations, may experience elevated extinction under elevated N levels (Stevens, Bunker, Schnitzer, & Carson, 2004; Xia & Wan, 2008). The deterministic loss of these clades across communities, in response to environmental changes, would promote community convergence, resulting in reduced taxonomic and phylogenetic β-diversity (Figure 1a). Phylogenetic β-diversity, however, may not necessarily decline as rapidly as taxonomic β-diversity if only some, not all species belonging to the same clades face extinction. Extinction, however, is far from deterministic (Lande, 1993; Lande, Engen, & Saether, 2003). The random loss of species, especially those with small population sizes (Matthies, Bräuer, Maibom, & Tscharntke, 2004; Suding et al., 2005), in different locations may drive divergence of species composition among communities, resulting in increased taxonomic and phylogenetic β-diversity (Figure 1b,c). Likewise, colonization could be either stochastic or deterministic, causing corresponding changes in taxonomic and phylogenetic β-diversity (Figure 1d,f,g). Colonization-induced changes in phylogenetic β-diversity also may not necessarily parallel those in taxonomic

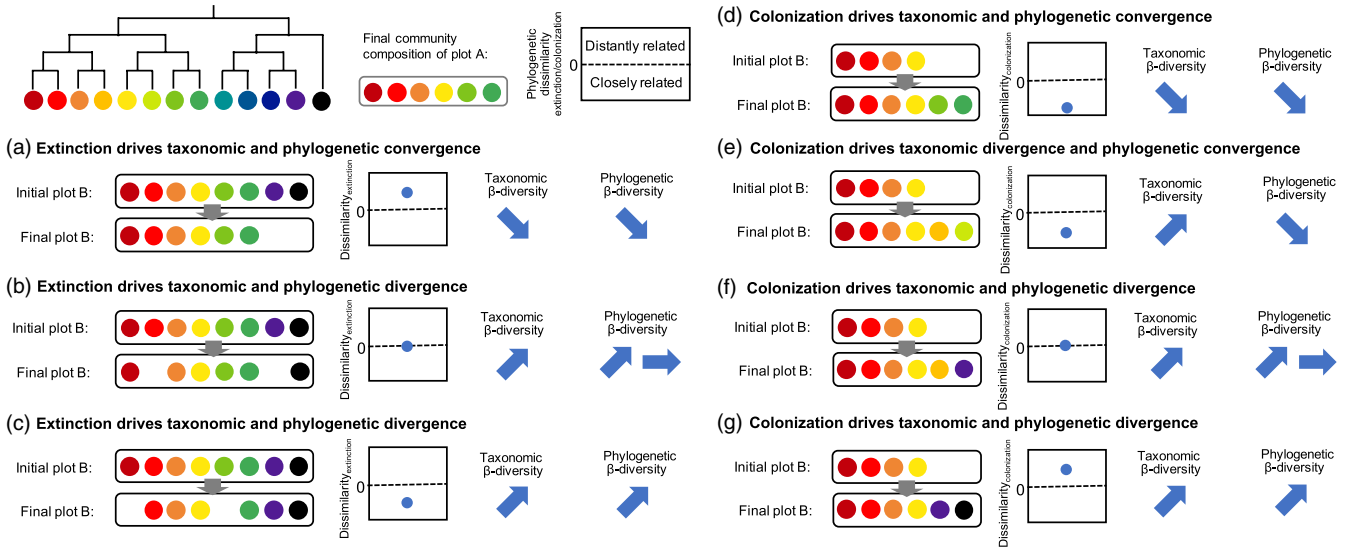

FIGURE 1 A conceptual diagram of the potential effects of species colonization and extinction on community taxonomic and phylogenetic beta diversity. Plot A and B are two replicate plots under the same experimental treatments. For illustration purpose, here we only relate colonization/extinction in plot B (focal plot) to communities in plot A (reference plot). The overall effects of species colonization and extinction on community taxonomic and phylogenetic beta diversity could be assessed by averaging all possible pairwise combinations of replicate plots that are subject to the same treatments. Phylogenetic dissimilarity$_{\text{colonization/extinction}}$ is the standardized effect size of phylogenetic β-diversity between colonized/extinct species in plot B and final community composition of plot A. (a) Extinction eliminates species in plot B that are distantly related to final species composition in plot A, leading to decreased taxonomic and phylogenetic beta diversity between the two plots. (b) Random extinction of species in plot B leads to increased taxonomic beta diversity and increased or unchanged phylogenetic beta diversity between the two plots. (c) Extinction eliminates species in plot B that are closely related to final species composition in plot A, leading to increased taxonomic and phylogenetic beta diversity between the two plots. (d) Colonization of species into plot B leads to similar final species composition in the two plots, leading to decreased taxonomic and phylogenetic beta diversity between the two plots. (e) Colonization of species into plot B that are not present in plot A but closely related to final species composition in plot A leads to increased taxonomic but decreased phylogenetic beta diversity between the two plots. (f) Random colonization of species into plot B leads to increased taxonomic beta diversity and increased or unchanged phylogenetic beta diversity between the two plots. (g) Colonization of species that are distantly related to final species composition in plot A into plot B leads to increased taxonomic and phylogenetic beta diversity between the two plots

β-diversity. For example the colonization of a group of species in which members are closely related would drive the communities towards phylogenetic convergence, but may not necessarily cause taxonomic convergence if other factors, such as dispersal limitation, prevent the same species from colonizing all localities. Under this circumstance, we would expect increased taxonomic β-diversity but decreased phylogenetic β-diversity (Figure 1e).

Here, we report on a field experiment, conducted in a temperate steppe in northern China, to investigate the effects of N and precipitation amendment on taxonomic and phylogenetic β-diversity of plant communities. The temperate steppe in this area is currently experiencing significant anthropogenic environmental changes, including increased N deposition and precipitation (Chen et al., 2013; Niu et al., 2010; Xia, Niu, & Wan, 2009), necessitating a thorough understanding of their ecological consequences. Previous work at the study site has documented changes in a number of community and ecosystem properties, including functional group composition (Yang et al., 2011), ecosystem productivity, respiration and net C exchange (Niu et al., 2009, 2010), community stability (Yang et al., 2012) and plant phylogenetic community structure (Yang et al., 2018), in response to experimental manipulations of N and precipitation. However, the question of how these environmental changes affect the trajectory of community assembly remains unanswered. We showed that both N and water addition increased the standard effective size of taxonomic β-diversity, whereas water, not N, addition, reduced the standard effective size of phylogenetic β-diversity, suggesting that anthropogenic environmental changes differentially affected plant community assembly trajectories at taxonomic and phylogenetic scales.

2 | MATERIALS AND METHODS

2.1 | Study site, experimental design and vegetation sampling

The experiment was conducted in a natural grassland at the Duolun Restoration Ecology Station of the Institute of Botany, Chinese Academy of Sciences, located in a temperate steppe (42°02' N, 116°17' E) in Inner Mongolia, China. The study area has a semi-arid continental monsoon climate with annual precipitation of 378 mm and mean annual temperature of 2.1°C. Dominant plant species (in terms of cover) in this area are perennial grasses and forbs, including

Stipa krylovii, *Artemisia frigida*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum* and *Agropyron cristatum*. Our study site was heavily grazed by livestock prior to 2001; it has been fenced since 2001 to exclude large herbivores.

The experiment used a split-plot design with N addition being the primary factor and water addition being the secondary factor. Four pairs of 45 × 28 m plots were established in 2005, with two plots in each pair assigned to the control and N addition treatments respectively. Within each plot, we set up two 15 × 10m subplots assigned to the control and water addition treatments respectively. N enrichment was accomplished by adding 10 g N/m^2 $year^{-1}$ in July 2005 in the form of urea and in July from 2006 to 2013 in the form of NH_4NO_3. The rate of natural N deposition in the study area is approximately 1.47 g N/m^2 $year^{-1}$ (Zhang et al., 2017), and the amount of N addition applied is comparable to the rate of atmospheric nitrogen deposition in the North China Plain (about 8.33 g N/m^2 $year^{-1}$; He, Liu, Fangmeier, & Zhang, 2007), where agricultural activities and fossil fuel consumption are more concentrated. Water addition was conducted by adding 15 mm of water weekly in July and August, resulting in an approximately 30% increase in water supply each year. More detailed information on the study area and experimental design can be found in Yang et al. (2012).

We surveyed the experimental plots in August each year from 2005 to 2013. In each plot, we placed a 1 × 1 m frame with 100 10 × 10 cm grids into a randomly selected 1 × 1 m quadrat. All species in each grid were identified and their coverage were estimated based on their occurrence within the 100 grids. We also collected data on key plant functional traits, including plant height, rooting depth, leaf N concentration and specific leaf area (SLA). Unlike our previous work (Yang et al., 2018), which extracted most trait data from the TRY database (Kattge et al., 2011), here we measured most data in situ. Plant height was measured as the maximum height of each species in the experimental plots at the beginning of the experiment. Plant samples for the measurement of other traits were collected from a nearby grassland outside the experimental plots. Rooting depth, leaf N concentration and SLA of 26 common species were measured according to Cornelissen et al. (2003). For species for which trait data were not directly measured, we extracted data on rooting depth, leaf N concentration and SLA from the TRY database (Supporting Information Figure S1; Kattge et al., 2011).

2.2 | Phylogenetic tree

We constructed a phylogenetic tree for the 52 species observed in the experimental area (Supporting Information Figure S1). First, we built a genus-level phylogenetic tree based on the phylogeny of vascular plants generated by Zanne et al. (2014) and Qian and Jin (2016). However, species in the genera *Allium*, *Astragalus* and *Potentilla* were absent from Zanne et al. and Qian & Jin's phylogeny. We thus extracted the ITS1 and ITS2 sequences of species belonging to these genera from GenBank and constructed a phylogenetic tree for each genus. We aligned the sequences from GenBank with Clustal X (version 2.0; Larkin et al., 2007), confirmed the alignment by observation, and selected the best evolution model with jModelTest (version 2.1.10; Guindon & Gascuel, 2003; Darriba, Taboada, Doallo, & Posada, 2012; 012,340 + G+F for *Allium* and *Potentilla*; 011,012 + F for *Astragalus*). The phylogeny of each genus was constructed with the Bayesian method in MrBayes (version 3.1.2; Huelsenbeck & Ronquist, 2001), using the closest relative to each genus as the outgroup.

2.3 | Species and phylogenetic β-diversities and their standardized effect sizes

To assess treatment effects on community convergence/divergence, we calculated dissimilarities in species composition (i.e. taxonomic β-diversity) and phylogenetic structure (i.e. phylogenetic β-diversity) between replicated plots within the same treatment. Taxonomic β-diversity was calculated using the abundance-weighted Bray–Curtis dissimilarity index (Bray & Curtis, 1957). The Bray–Curtis index is robust to sampling errors (Schroeder & Jenkins, 2018), and is widely used to quantify taxonomic β-diversity among communities. The value of Bray–Curtis dissimilarity approaches 0 when species composition is identical, and approaches 1 when species composition is completely different. Phylogenetic β-diversity was quantified using the abundance-weighted pairwise dissimilarity index D_{pw} (Swenson, 2011; Webb, Ackerly, & Kembel, 2008). D_{pw} is suitable for detecting phylogenetically basal turnover between communities and converges to the Bray–Curtis dissimilarity index in the case of a star phylogeny (Swenson, 2011). It is calculated as:

$$D_{pw} = \frac{\sum_{i=1}^{n_{k_1}} f_i \overline{\delta_{ik_2}} + \sum_{j=1}^{n_{k_2}} f_j \overline{\delta_{jk_1}}}{2} \quad (1)$$

where k_1 and k_2 are two communities, f_i is the relative cover of species i in community k_1, f_j is the relative cover of species j in community k_2, $\overline{\delta_{ik_2}}$ is the mean pairwise phylogenetic distance between species i in community k_1 and all species in community k_2 excluding conspecific species and $\overline{\delta_{jk_1}}$ is the mean pairwise phylogenetic distance between species j in community k_2 and all species in community k_1 excluding conspecific species. Larger values of D_{pw} indicate greater phylogenetic distance between the compared communities.

In addition to niche-based and stochasticity-based ecological processes, the observed patterns of taxonomic and phylogenetic β-diversity may also be affected by both local community diversity (α-diversity) and the size of the regional species pool (γ-diversity). In particular, when the regional species pool remains unchanged, any factor that changes α-diversity could potentially alter β-diversity owing simply to random sampling effects (Anderson et al., 2011; Chase, Kraft, Smith, Vellend, & Inouye, 2011; Chase & Myers, 2011; Myers et al., 2013). Therefore, we performed null model analyses to disentangle the variation in β-diversity from variation in α-diversity. The null model analyses determined if the observed patterns in taxonomic and phylogenetic β-diversity deviated from the expectations of random assembly, after accounting for changes in α-diversity. A null distribution of taxonomic β-diversity was generated by randomly sampling individuals from the

regional species pool 999 times, while persevering the total plant cover in each plot and the relative cover of each species in the species pool (Kraft et al., 2011). Null distributions of phylogenetic β-diversity were generated by randomizing the names of species across the tips of the phylogenetic tree 999 times (Webb et al., 2008). Standardized effect size (SES; Gotelli & Graves, 1996) was calculated for taxonomic (β-deviation) and phylogenetic (SES.D_{pw}) β-diversity using the mean and standard deviation of their respective null distributions:

$$\mathrm{SES}.X = \frac{X_{\mathrm{obsered}} - \overline{X_{\mathrm{null}}}}{\mathrm{sd}\left(X_{\mathrm{null}}\right)} \quad (2)$$

where X_{observed} is the observed β-diversity value between two communities, $\overline{X_{\mathrm{null}}}$ is the mean value of the null distribution and sd (X_{null}) is the standard deviation of the null distribution. Positive and negative values indicate higher and lower β-diversity than expected by chance, respectively, whereas a value of zero indicates that the observed β-diversity does not differ from random patterns.

2.4 | Species colonization and extinction

We classified a species to be locally extinct from a plot if they were present in 2005 but absent in 2013, and defined new colonists as species that were absent in 2005 but present in 2013 in a plot. To examine the effect of new colonists on the taxonomic and phylogenetic dissimilarity among plots within a treatment, we calculated the average β-deviation and phylogenetic SES.D_{pw} between new colonists in each replicate plot and final species composition in the three other replicate plots under the same treatment (β-deviation(C) and SES.D_{pw}(C)). A negative β-deviation(C) or SES.D_{pw}(C) indicates that new colonists in a plot are more similar or phylogenetically more closely related to the species composition in other plots of the same treatments than expected by chance respectively. To examine the effect of the extinct species on the taxonomic and phylogenetic dissimilarity among plots within a treatment, we calculated the average β-deviation and phylogenetic SES.D_{pw} between extinct species in each replicate plot and the final species composition in the other replicate plots under the same treatment (β-deviation(E) and SES.D_{pw}(E)). For species extinction, a positive β-deviation(E) or SES.D_{pw}(E) indicates that the extinct species in a plot are more dissimilar or phylogenetically more distantly related to the remaining species in other plots of the same treatments than expected by chance respectively. To address the possibility that the results based on 2005 and 2013 only may be vulnerable to observation error, we also divided the experiment into three periods (2005–2007, 2007–2010 and 2010–2013), and analysed β-deviation(C/E) and SES.D_{pw}(C/E) for each period. Consistent results between the three periods would lend greater credibility to our results.

To assess the contributions of species' functional traits on the pattern of SES.D_{pw}, we calculated SES.D_{pw} values of functional traits for both colonist and extinct species using the dendrograms of the measured functional traits (i.e. plant height, rooting depth, leaf N concentration and SLA). We generated four trait dendrograms, one for each functional trait, using UPGMA clustering based on the Euclidean distance matrix (Petchey & Gaston, 2002).

2.5 | Statistical analysis

To test for the effects of N and water addition on taxonomic and phylogenetic β-diversity and their standardized effect sizes over time, we conducted a permutational multivariate analysis of variance (PERMANOVA; 999 permutations; Anderson, 2001) in which fertilization, watering, time and their interactions were used as explanatory variables. Following PERMANOVA, we also used permutational analysis of multivariate dispersions (PERMDISP) to test whether communities differ in their within-treatment dissimilarities (Anderson, 2006; Anderson, Ellingsen, & McArdle, 2006).

We calculated the phylogenetic signal of the four functional traits measured in this study using the *K* statistic (Blomberg, Garland, & Ives, 2003). The significance (p-values) of the phylogenetic signal was evaluated by comparing the variance of independent contrasts for each trait to the expected values obtained by shuffling leaf trait data across the tips of the phylogenetic tree 999 times. To assess the importance of species' initial coverage and functional traits on colonization and extinction, we ran logistic regressions of species colonization/extinction as a function of species' initial coverage and trait values (i.e. plant height, rooting depth, leaf N concentration and SLA). Species that did not colonize or go extinct in any plot within a treatment were assigned a value of 0. Otherwise, species were assigned a value of 1. We assigned values for colonization and extinction separately.

All analyses were performed using R 3.5.1 (R Core Team., 2018). The Bray–Curtis index was calculated using the *vegdist* function in the package *vegan* (Oksanen et al., 2018), and D_{pw} was calculated using the *comdist* function in the package *picante* (Kembel et al., 2010). The null communities were generated using the *nullmodel* in the *vegan* package (Oksanen et al., 2018). PERMANOVA and PERMDISP were performed using the functions *adonis2* and *betadisper in the vegan* package respectively (Oksanen et al., 2018). The analyses on phylogenetic signal were conducted using the function *multiPhylosignal* in the *picante* package (Kembel et al., 2010).

3 | RESULTS

3.1 | Species taxonomic and phylogenetic β-diversity, and their standardized effect size

Taxonomic β-diversity (Bray–Curtis index) fluctuated significantly over time in all but the water addition treatments. Taxonomic β-diversity exhibited a positive trend only in the N addition treatment, resulting in greater β-diversity in this treatment than the controls (Figure 2a). Phylogenetic β-diversity (D_{pw}) remained largely unchanged in the N addition and N + water addition treatments, but declined over time in the control and water addition plots, resulting in greater phylogenetic β-diversity in the N addition and N + water

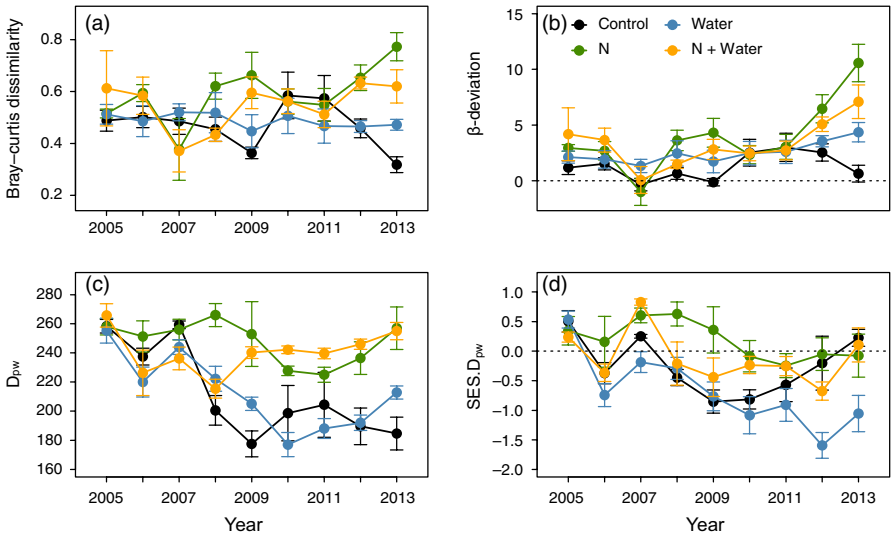

FIGURE 2 Changes in taxonomic β-diversity, phylogenetic β-diversity and their respective standardized effect sizes among replicate plots within each treatment over time. Taxonomic β-diversity and its standardized effect size were measured by (a) Bray–Curtis dissimilarity and (b) β-deviation respectively. Phylogenetic β-diversity and its standardized effect size were measured by (c) D_{pw} and (d) $SES.D_{pw}$ respectively. Values are mean ± standard error. The standardized effect sizes (β-deviation and $SES.D_{pw}$) show the magnitude of deviation between observed β-diversity and the values generated from null models. Negative values indicate lower β-diversity than expected from chance, whereas positive values indicate the opposite

addition plots towards the end of the experiment (Figure 2c). PERMANOVA indicated that N enrichment, water addition, year and all their two-way interaction terms significantly affected taxonomic β-diversity, whereas phylogenetic β-diversity was only significantly affected by N addition (Table 1). PERMDISP revealed that N, water and N + water addition treatment increased the dispersion of species composition (Supporting Information Figure S2).

β-deviation showed a similar temporal pattern as the Bray–Curtis index. At the end of the experiment, β-deviation was not significantly different from null expectation in the control plots, but was significantly higher than null expectation in the N, water and N + water addition treatments, with the highest values observed for the N addition plots (Figure 2b). The standardized effect size of D_{pw} (i.e. $SES.D_{pw}$) was significantly greater than zero in all treatments initially (one-sample *t*-test, $p < .05$). At the end of the experiment, however, $SES.D_{pw}$ was significantly negative (one-sample *t*-test, $p = .018$) in the water addition plots and not significantly different from zero in the other treatments (one-sample *t*-test, $p > .05$; Figure 2d). Correspondingly, PERMANOVA indicated that N enrichment, water addition and their interaction terms significantly affected β-deviation and that $SES.D_{pw}$ was only affected by water addition (Table 1). PERMDISP revealed that D_{pw} showed greater dispersion in the N, water and N + water addition treatments than the controls, whereas SES. D_{pw} showed lower dispersion in the water addition treatment than other treatments (Figure S2, Table S1).

3.2 | Species colonization and extinction

In the control plots, most of the extinct species were forbs from the genera *Allium* and *Potentilla* and most colonists were grasses from the family Poaceae. In plots with N fertilization, in addition to species that went extinct in the controls, some grasses from the family Poaceae and Cyperaceae also went extinct; the few colonists were mainly forbs from the families Rosaceae and Cruciferae. In the water addition plots, however, the number of extinct species was much lower, with most being extinct also in the control plots. Species

TABLE 1 Results of permutational multivariate analysis of variance (PERMANOVA) on the effects of N enrichment, water addition, year and their interactions on community taxonomic β-diversity (Bray–Curtis), phylogenetic β-diversity (D_{pw}) and their respective standard effect sizes (β-deviation and SES. D_{pw}). The analyses were performed using 999 permutations. $p < 0.05$ shown in bold.

		Bray–Curtis		D_{pw}		β-deviation		$SES.D_{pw}$	
	Df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
N	1	20.45	**.001**	11.62	**.001**	1.79	**.001**	0.87	1.000
Water	1	5.21	**.001**	1.17	0.181	1.15	**.001**	1.02	**.035**
Year	1	12.42	**.001**	1.55	0.055	1.00	.467	0.98	.924
N:W	1	2.69	**.016**	1.10	0.212	1.08	**.032**	0.99	.858
N:Y	1	3.69	**.002**	1.63	**0.047**	1.16	**.003**	1.00	.614
W:Y	1	2.66	**.011**	1.30	0.113	1.10	**.012**	1.01	.110
N:W:Y	1	1.02	.382	0.92	0.499	1.00	.500	0.99	.765

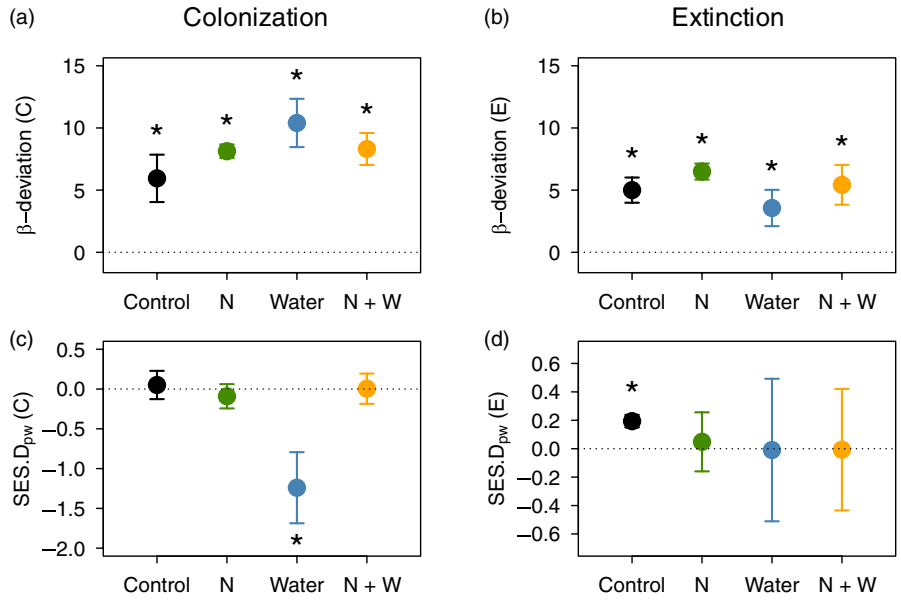

FIGURE 3 The taxonomic (β-deviation) and phylogenetic dissimilarity (SES.D$_{pw}$) between (a, c) new colonists and (b, d) extinct species of each plot and final species composition in the other three replicate plots within the same treatment. For species colonization, a negative β-deviation(C) indicates that new colonists are more similar to the final communities in other replicates than expected by chance, and a negative SES.D$_{pw}$(C) indicates that new colonists are more phylogenetically closely related to the final communities in other replicates than expected by chance, indicating deterministic colonization. For species extinction, a positive β-deviation(E) indicates that extinct species are more dissimilar to the remaining species in other replicates than expected by chance, and SES.D$_{pw}$(E) indicates that extinct species are more phylogenetically distantly related to the remaining species in other replicates than expected by chance, indicating deterministic extinction. * denotes values that are significantly different from zero based on one-sample *t* test ($p < .05$). Error bars represent standard errors

colonizing the water addition plots were mainly forbs from the families Labiatae, Gentianaceae and Leguminosae (Figure S1).

The compositional dissimilarity between colonists and final community composition within a treatment (i.e. β-deviation(C)) was significantly greater than zero in all treatments, indicating that colonists were more dissimilar to species in other replicate plots than null expectation (Figure 3a; one-sample *t*-test, $p < .05$). The compositional dissimilarity between extinct species and the final community composition within a treatment (i.e. β-deviation(E)) was also significantly greater than zero in all treatments (Figure 3b; one-sample *t*-test, $p < .05$), indicating taxonomically deterministic extinction. The phylogenetic SES.D$_{pw}$ between colonists and final community composition within a treatment (i.e. SES.D$_{pw}$ (C)) did not significantly differ from zero in the control, N addition and N + water addition treatments (Figure 3c; one-sample *t*-test, $p > .05$), indicating phylogenetic randomness of species colonization in these treatments. However, we found significant negative phylogenetic SES.D$_{pw}$(C) in the water addition treatment (Figure 3c; one-sample *t*-test, $p = .035$), indicating that colonizing species in each water addition plot were more closely related to species in other replicate plots than expected by chance. The phylogenetic SES.D$_{pw}$ between extinct species and final community composition within a treatment (SES.D$_{pw}$(E)) was not significantly different from zero in the N, water and N + water addition treatments (Figure 3d; one-sample *t*-test, $p > .05$), indicating phylogenetic randomness of species extinction in these treatments. The average phylogenetic SES.D$_{pw}$(E) in the controls was significantly greater than zero (Figure 3d; one-sample *t*-test, $p = .011$), indicating that extinction excluded species that were more phylogenetically distantly related to the final species composition than expected by chance in this treatment. When the experiment was divided into three periods (2005–2007, 2007–2010 and 2010–2013), the patterns for β-deviation(C/E) and SES.D$_{pw}$(C/E) within each period were similar to those across all years (Figure S3).

Among the four functional traits measured in this study, significant phylogenetic signal was detected only for leaf N concentration ($p = .035$, Table S1). Therefore, we presented the results on leaf N concentration in the main text and the results on other functional traits in the supporting information (Supporting Information Figure S4, S5, Appendix A, B). The SES.D$_{pw}$(C) for leaf N concentration showed a similar pattern with phylogenetic SES.D$_{pw}$(C), such that colonizing species in each water addition plot were more similar in leaf N concentration with species in other replicate plots than expected by chance (Figure 4a, one-sample *t*-test, $p = .036$). For species extinction, non-significant SES.D$_{pw}$(E) for leaf N concentration was found for all treatments (Figure 4b).

The initial coverage of species was a significant predictor of species extinction in all treatments. Species with lower initial coverage tended to have a greater probability of extinction (Figure 5a–d), corresponding with the taxonomically deterministic extinction found in all treatments (shown in Figure 3b). Leaf N concentration affected the likelihood of species colonization in the water addition treatment, such that species with higher leaf N concentrations were more likely to colonize (Figure 5g). In the N + water addition treatment, leaf N concentration affected the likelihood of species extinction,

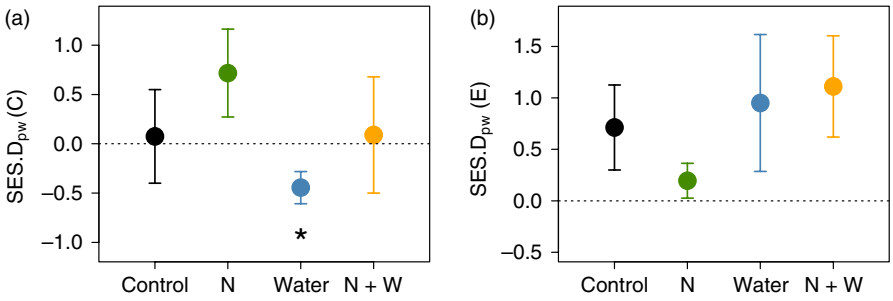

FIGURE 4 The functional trait dissimilarity (SES.D_{pw}) for leaf N concentration between new colonists (a) and extinct species (b) of each plot and final species composition in the other three replicate plots within the same treatment. A negative SES.D_{pw}(C) indicates that new colonists are more similar to the final species composition than expected by chance. A positive SES.D_{pw}(E) indicates that extinct species are more different from the remaining species than expected by chance. * denotes values that are significantly different from zero based on one-sample *t* test ($p < .05$). Error bars represent standard errors

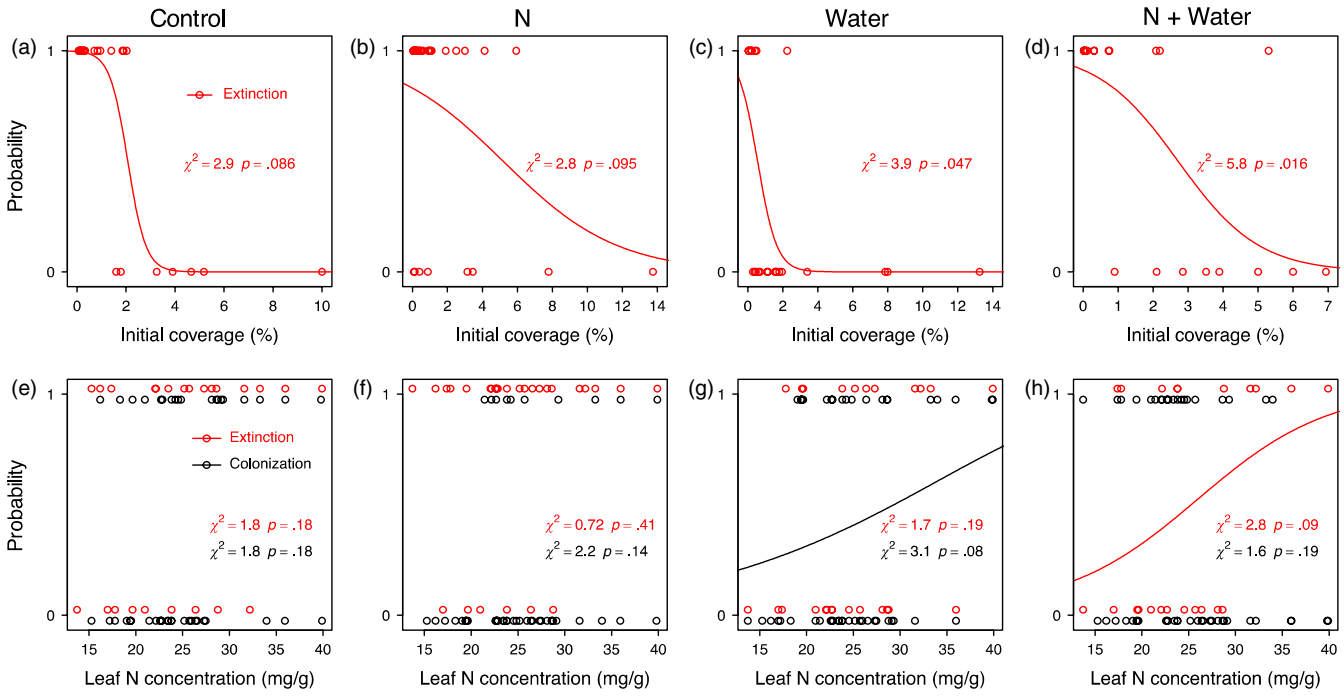

FIGURE 5 Species colonization (black circles) and local extinction (red circles) as functions of initial coverage (a–d) and leaf N concentration (e–h) in each treatment. Species that did not colonize or go extinct in any plot within a treatment was assigned a value of 0. Otherwise, species were assigned a value of 1. Significant logistic regression lines ($p < .1$) are shown

such that species with higher N concentration suffered from greater risk of extinction (Figure 5h).

4 | DISCUSSION

The Earth's ecosystems are facing widespread anthropogenic environmental changes. A key challenge is to elucidate how ecological processes interact with evolutionary processes in influencing diversity patterns across spatial scales in the face of anthropogenic environmental changes. In this study, we investigated the impact of elevated N deposition and precipitation on species taxonomic and phylogenetic β-diversity, and linked species colonization and extinction to the observed β-diversity patterns. We found that both N enrichment and water addition significantly increased taxonomic β-diversity, and N enrichment also significantly increased phylogenetic β-diversity. However, when the differences in local community size were controlled for using null models, both N enrichment and water addition significantly increased the standard effect size of taxonomic β-diversity (i.e. β-deviation), suggesting that resource enrichment led to increased taxonomic divergence; water addition, not N enrichment, significantly decreased the standard effect size of phylogenetic β-diversity (i.e. SES.D_{pw}), suggesting that water addition drove communities to converge towards more similar phylogenetic structure.

A number of experiments have assessed the effects of resource addition on taxonomic β-diversity. Chalcraft et al. (2008)

synthesized data from 18 N-enrichment experiments along a productivity gradient across North America, and found that N addition promoted β-diversity at low-productivity sites but reduced β-diversity at high-productivity sites, with the threshold productivity around 400 g m^{-2} $year^{-1}$. The positive treatment effects on β-diversity in our experiment are in accordance with this general pattern, as the productivity at our study site is far below the threshold (60 ~ 250 g m^{-2} $year^{-1}$, Xu et al., 2018). N and water are known to be the two major limiting resources for our study grassland (Bai, Han, Wu, Chen, & Li, 2004; Niu et al., 2010). Our results are thus consistent with the idea that adding limiting resources enhances β-diversity in resource-scarce environments, where strong environmental filtering limits community membership in a largely deterministic manner (Chalcraft et al., 2008; Chase, 2010). Note that in our experiment, both taxonomic β-diversity and β-deviation increased in response to N and water addition, indicating that the observed community divergence after N and water addition was due to the enhanced role of stochastic processes rather than changes in α-diversity. One possible mechanism for the more important role of stochastic assembly processes under resource enrichment is that stronger priority effects may lead to the increased likelihood of multiple community states in more benign environments (Chase, 2003, 2007, 2010). In our study, dispersal was highly stochastic at the species level, as evidenced by the compositional dissimilarity between colonized species in each plot and species in other replicate plots (i.e. β-deviation (C)) being much higher than null expectation in all treatments. Under resource amendment, such stochastic dispersal may have led to high variability in species arrival history and, in turn, strong priority effects, promoting the taxonomic divergence of communities (Chase, 2010; Vannette & Fukami, 2017).

We found that water addition, rather than N enrichment, significantly decreased the standard effect size of phylogenetic β-diversity ($SES.D_{pw}$), driving the communities from being phylogenetically divergent to being phylogenetically convergent (Figure 2d). Such transition in the water addition treatment could be attributed to the phylogenetically non-random colonization of species. Specifically, the colonists in each plot after water addition were significantly related to species in other replicate plots (Figure 3c), resulting in phylogenetically similar community composition among plots. This pattern contrasts with the taxonomically stochastic colonization and divergence observed in the water addition plots (see the previous paragraph), supporting our hypothesis that taxonomic and phylogenetic β-diversity may not necessarily respond similarly to environmental changes (Graham & Fine, 2008; Hardy et al., 2012). These results emerged likely because water addition favours certain closely related species with similar traits (e.g. those with similar leaf N content, Figure 4a), resulting in community convergence at the phylogenetic scale, but facilitates the non-deterministic colonization of these species among plots (Figure 3a), resulting in community divergence at the species level. One way to confirm this explanation is to eliminate the stochasticity associated with species colonization by, for example seed addition, which would favour community convergence at both taxonomic and phylogenetic scales. Indeed, a recent study has found that fertilization and water addition into a California grassland reduced plant taxonomic β-diversity when seeds of common species were added to all experimental plots (Eskelinen & Harrison, 2015). On the other hand, our results clearly show that considering both phylogenetic and taxonomic turnover allows a better assessment of the role of deterministic and stochastic processes in shaping ecological communities.

We found evidence for functional trait-based species colonization in the water addition plots. Leaf N concentration, the only plant trait that exhibited significant phylogenetic signal (Table S2), was found to be more similar between the colonist in each plot and the species in other replicate plots in the water addition, but not other treatments (Figure 4a). Correspondingly, the probability of colonization was strongly associated with leaf N concentration, with N-rich species tending to have a greater probability of colonization (Figure 5g). Leaf N concentration is a key functional trait on the "leaf economic spectrum" that relates to plant resource capture and conservation (Wright et al., 2004). N-poor species are generally conservative in resource use and expected to be better at coping with abiotic stress (Coley, Bryant, & Chapin, 1985; Díaz et al., 2016; Reich, Walters, & Ellsworth, 1997; Wright et al., 2004). Studies that explored relationships between leaf economic traits and climate have found a general tendency for species inhabiting arid and semi-arid regions to exhibit a more conservative strategy in resource use (Wright, Reich, & Westoby, 2001). In line with these findings, our result demonstrated that enhanced water supply alleviated abiotic stress and facilitated species on the "acquisitive" end of the leaf economic spectrum to colonize, which resulted in phylogenetic homogenization among water addition plots. Finally, we note that traits of the same plant species may respond to resource amendment, such that they may also differ among experimental treatments (Yan et al., 2015). This possibility, however, would need to be addressed by future studies, as we only quantified plant traits in the controls.

Our study provides, to our knowledge, the first experimental evidence that anthropogenic environmental changes can differentially affect plant taxonomic and phylogenetic β-diversity. Both N enrichment and water addition significantly increased taxonomic β-diversity, whereas water addition, not N enrichment, significantly reduced phylogenetic β-diversity, with the latter attributed to colonizing species in each water addition plot being more closely related to species in other replicate plots of the same treatment. Our results thus illustrate that although stochastic processes may cause communities to diverge more in species composition under anthropogenic environmental changes, deterministic processes could still produce communities more convergent in phylogenetic community structure. It remains to be seen whether these findings apply to other systems and whether they extend to ecosystem functions. For example an interesting question to ask next is whether community phylogenetic convergence under precipitation amendment would translate into ecosystem functional convergence.

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AUTHORS' CONTRIBUTIONS

S.W., L.J. and X.Y. conceived the project; G.L, D.S., H.S., M.Z., Z.Z., J.S. and J.R. carried out the field experiments and collected data; X.Y. analysed the data; X.Y. and L.J. wrote the first draft of the manuscript; all authors contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nh1s3k3 (Yang et al., 2019).

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