

Phylogenetic diversity is maintained despite richness losses over time in restored tallgrass prairie plant communities

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Summary

1. Ecosystem restoration is an important tool for mitigating biodiversity loss and recovering critical ecosystem services to humanity, but restoration rarely takes into account the evolutionary attributes of the community being restored. Phylogenetic diversity (PD) represents a potentially valuable measure of restoration success because it can correlate with functional trait diversity that drives ecosystem function. However, PD patterns in restored communities are rarely assessed.

2. We surveyed plant communities in restored tallgrass prairies 2–19 years old and calculated two PD measures, SES_{MNTD} and SES_{MPD} , of the communities and seed mixture applied to sites. We also identified high-threat exotic species present in each site to determine whether PD of the seed mixture applied was related to resistance against invasion.

3. We show that PD in North American tallgrass prairie restorations, as measured by both SES_{MNTD} and SES_{MPD} , is maintained over time even as richness declines. Neither the resulting community PD nor invasion by high-threat exotic species was affected by PD of the seed mixture used in site restoration. Thus, simply maximizing PD of seed mixtures without considering the particular component species is unlikely to help achieve restoration goals.

4. *Synthesis and applications.* These results suggest that species losses over time are not biased towards species with or without close relatives in the community. If phylogenetic diversity (PD) reflects functional trait diversity in communities, then local declines in species richness may not necessarily mean the loss of ecosystem function in restoration projects. However, PD of restored communities may be limited by low establishment rates for most species. Conservation practitioners should consider PD with careful planning to maintain overall community diversity and potentially maximize ecosystem function and services in restorations. This perspective will require a deeper understanding of the relationships between phylogenetic relatedness and traits associated with competition and fitness.

Key-words: above-ground net primary productivity, biodiversity, competition, ecosystem function, ecosystem services, grassland, invasive species, phylogenetic diversity, restoration, tallgrass prairie

Introduction

Habitat loss and degradation are the leading causes of global biodiversity loss (Tilman *et al.* 2001; Pereira, Navarro & Martins 2012), and these losses have impor-

tant implications for humanity because species extinctions and associated ecosystem damage have resulted in the delivery of fewer ecosystem services for people (Chapin *et al.* 2000; Cardinale *et al.* 2012; Hooper *et al.* 2012). Beyond preserving remaining habitats, ecosystem restoration has become widely recognized as an essential strategy for stemming biodiversity losses and repairing the ecosystem functions that provide these services (Benayas *et al.*

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2009; Palmer & Filoso 2009; Bullock *et al.* 2011). Ecosystem restoration seeks to re-establish diverse, functioning ecosystems (Hobbs & Harris 2001; Thorpe & Stanley 2011), yet successfully re-establishing systems that maintain high biodiversity and function remains a significant challenge due to other global change pressures (e.g. invasive species and climate change) and limited understanding of the relationship between restored community composition and ecosystem functions (Chapin *et al.* 2000; Bonet & Pausas 2004).

Robust ecological functioning requires a functionally diverse community of organisms with a wide variety of traits that allows increased resource partitioning (Tilman *et al.* 1997; Cadotte, Carscadden & Mirotchnick 2011; Cardinale 2011). Because evolutionarily related species tend to share similar traits, community phylogenetic diversity (PD) – measures of the total evolutionary history represented by an assemblage of species (Faith 1992) – has become recognized as a potentially powerful predictor of function (Webb *et al.* 2002; Flynn *et al.* 2011; Srivastava *et al.* 2012). Furthermore, the widespread availability of phylogenetic information today, which has facilitated the integration of community ecology with evolutionary biology (Cavender-Bares *et al.* 2009), might make PD easier to measure than functional diversity indices that require species-by-species measurements of a large number of traits (Venail *et al.* 2015). PD encompasses the evolutionary history of functional trait diversity, so it may better reflect this history than a multivariate measure based on a subset of traits identified *a priori* by researchers (Cadotte, Cardinale & Oakley 2008; Cadotte *et al.* 2009; Cavender-Bares *et al.* 2009). However, this depends in part on assumptions of phylogenetic niche conservatism and the absence (or rarity) of convergent traits (Wiens & Graham 2005; Cooper, Freckleton & Jetz 2011; Araya *et al.* 2012), which have been questioned (Gerhold *et al.* 2015).

Plant community PD may be correlated with a number of community characteristics. Although numerous metrics to quantify PD exist, such as total phylogenetic history (total summed branch lengths) and other measurements that are less dependent on richness [e.g. mean pairwise distance (MPD) and mean nearest tip distance (MNTD), both used in this study], analyses have found that communities with greater PD in general can have greater productivity (Flynn *et al.* 2011; Cadotte 2013) and stability (Cadotte, Dinnage & Tilman 2012) than communities with lower PD, although these patterns are not universal (Venail *et al.* 2015). Communities with higher PD also may be more resistant to invasion (Lososová *et al.* 2015) and support increased animal diversity (Dinnage *et al.* 2012). These two goals are of particular importance for restoration ecology: invasions by exotic plant species are recognized as a major cause of biodiversity loss and one of the most serious threats to successful ecosystem restoration through the competitive exclusion of native species (McKinney & Lockwood 1999; Van Der Wal *et al.* 2008). Further, it is often assumed that animals and other

non-plant organisms will establish in restorations on their own through natural dispersal (Hilderbrand, Watts & Randle 2005; Wodika & Baer 2015). Despite its potential importance as an informative metric of ecosystem recovery, PD is rarely, if ever, assessed in restoration programmes. If PD or its perceived benefits are stated goals for restoration activities, then planting a species assemblage with greater PD could be a strategy for restoration practitioners to employ (Hipp *et al.* 2015).

We report here on an analysis of plant PD in a large-scale restoration project of North American tallgrass prairie. Tallgrass prairies are among the most endangered habitats on Earth, with more than 90% of original habitat converted to agriculture and other land uses (Samson & Knopf 1994). Using a chronosequence of sites ranging from 2 to 19 years since restoration, we surveyed plant communities, constructed a phylogeny of the species pool, including planted species, and calculated the PD of each site as well as the PD of seed mixtures applied to the majority of sites. Grassland restorations frequently lose species richness over time as individual species go locally extinct. Depending on how these extinctions are distributed across the tree of life, this may also represent lost PD, but this has not been investigated before. Thus, maintaining diversity in restorations as they age is a restoration goal, and research on how communities change over time following restoration is needed. We addressed four questions in this study: (i) Does plant community PD change following restoration? (ii) How is the resulting community PD influenced by the mixture of seeds applied at the time of planting and precipitation in the planting year? (iii) Does a more phylogenetically diverse seed mixture increase resistance against exotic invasion? (iv) Is productivity [above-ground net primary productivity (ANPP)] related to seed mixture PD?

Materials and methods

SITE SELECTION AND SURVEYS

This research occurred at The Nachusa Grasslands, a preserve in northern Illinois owned and managed by The Nature Conservancy (TNC), consisting mostly of restored and remnant (never ploughed) tallgrass prairie with some oak savanna and wetland patches interspersed. The area was used as pasture by 1873, converted to row crops by 1939, and sites remained in row-crop production (generally maize–soya bean rotation) until restoration. Restoration activities under TNC began in 1987, and the earliest site included in this study was restored in 1988. We chose 19 restorations ranging from 2 to 19 years since the cessation of agriculture and planting with seeds of native prairie species (see Table S1, Supporting information), ranging in size from 1.1 to 17.4 ha (mean \pm 1 SE, 7.4 ± 1.2). Sites were kept in crop rotation with the suppression of non-crop plants until restoration activities began, so native plant communities initially were entirely absent at each site. Sites were planted with a diverse mixture of native seeds collected largely or entirely from remnants or other restorations at Nachusa, and managers provided lists of all

species included in the seed mixes applied to 16 of the 19 sites (Table S2). Seed species lists for the remaining three sites were not available, and these sites were omitted from all analyses involving seed mixture PD. Although each site has its own unique history, restoration techniques and management activities were applied consistently to all sites from the start of restoration to the study year (1987–2005) (B. Kleiman, pers. comm.). These activities included prescribed burns on a 2- to 3-year rotation, and the youngest sites were burned at least once between planting and vegetation surveys. At all sites, managers surveyed annually for high-priority exotic species (described below), which were controlled using both herbicide application and physical removal. There also was no cattle or bison grazing on these sites during the study period, which can be an important source of heterogeneity in tallgrass prairie (Knapp *et al.* 1999).

We surveyed vegetation between 30 June and 14 August 2005 using a 20 × 50 m modified Whittaker plot (Barnett & Stohlgren 2003) randomly placed in each of the 19 sites at least 20 m from an edge. We identified all plant species in the plot to record presence. ANPP was determined by clipping vegetation from 0.1-m² quadrats within 10 subplots at each site and drying to determine biomass. During the year, these plant surveys were performed (2005), mean temperature was 11.5 °C and 753 mm of precipitation fell; this is slightly warmer and dryer than annual averages (8.5 °C and 947 mm, respectively). Additional site details and survey methods are described in more detail in Hansen & Gibson (2014). We did not compare these restored communities to remnants at the site because the remnants occur in different edaphic conditions (rocky areas that could not be ploughed) and thus are not representative of the environmental conditions in the restoration sites.

PHYLOGENY ESTIMATION

All plant species included in field sampling data from Nachusa Grasslands and from the grassland restoration seed mixtures were combined for a total list of 281 species (Hansen 2009; Hansen & Gibson 2014). A community phylogeny was inferred for these species (Fig. 1). Curated and banked coding sequences for two chloroplast loci, the large subunit of Rubisco (*rbcL*) and maturase K (*matK*), were acquired for each species from the NCBI GenBank data base. Two other loci that were screened, chloroplast *trnL-F* and nuclear ITS, proved to be too variable to retrieve monophyletic plant families. Species that were not represented in the data base were substituted when possible with congeneric species native to North America for which sequences were available (Tables S3–S4). Genes substituted from these congeners acted as phylogenetic placeholders, and 268 of 281 species were represented in the phylogeny (Table S5). The two sets of gene sequences were aligned using ClustalW (Thompson, Higgins & Gibson 1994). Alignments were then inspected visually to omit sequences that were clearly misidentified. The aligned *rbcL* and *matK* sequences were then concatenated for phylogenetic analysis. GenBank accession numbers for *rbcL* and *matK* sequences used in phylogeny construction are presented in the Supplemental Materials (Tables S3–S4).

Bayesian inference was used to estimate phylogeny as implemented in MrBayes v 3 (Ronquist & Huelsenbeck 2003). Dirichlet priors were used for base frequencies and the rate matrix. Uniform priors were used for the shape parameter (ALPHA), proportion of invariable sites (I) and topology. A Markov chain Monte Carlo analysis was run to completion for 2 × 10 000 000 generations with four chains each. *Equisetum hyemale* was even-

tually omitted from the analysis as it exhibited an unexpected phylogenetic position embedded within the eudicots. Note that *E. hyemale* was the only non-seed plant on the checklist, and it had highly divergent nucleotide sequences. Including *E. hyemale* in our analyses would artificially inflate the PD measurements in any site where it was observed.

PD ANALYSES

Using the phylogeny described above, we calculated PD of the communities and seed mixes for each site with the package 'picante' (Kembel *et al.* 2010) in R. We calculated two measures of PD each for both plant communities and seed mixes: MPD, the average of the distances between all pairs of species in the community; and MNTD, the average of the distances between each species and its nearest relative in the community. Because these values frequently correlate with richness, we used richness-independent standardized effect sizes for each metric, SES_{MPD} and SES_{MNTD}. These values were calculated by comparing either MPD or MNTD to a null mean value generated by randomizing species across tips of the phylogeny 999 times. For simplicity, hereafter we refer to SES_{MPD} and SES_{MNTD} as MPD and MNTD, respectively.

STATISTICAL ANALYSES

To determine how species richness and each measure of PD changed over time following initial restoration, we used generalized linear models (GLMs) with Gaussian error distribution and identity link, treating age of restoration as a fixed independent variable and richness, MPD, and MNTD as dependent variables. To test the hypotheses that the PD of the seed mixture applied at restoration and the precipitation in the first year affect the plant community that results, we used GLMs as above, treating seed mixture MPD or MNTD and summer precipitation (mm, sum of May through August) in the first year of growth as fixed independent variables and community MPD and MNTD as dependent variables. Precipitation in the first year is an important determinant of native species establishment in grasslands (Bakker *et al.* 2003). Historical precipitation data were obtained from a nearby weather station (Dixon, Illinois, approximately 12 km away). Seed mixture species composition varied over the years, so we determined whether seed mixture PD (both MPD and MNTD) varied across the 17 years of restoration included here by analysing seed mixture MPD or MNTD using GLMs with age as a fixed independent variable. We evaluated independent variables with Wald *t*-tests, and all analyses were carried out in R.

To further understand how seed mixture composition influenced the resulting plant community, we identified the species that were most likely to establish in plantings when applied at restoration. We limited the analyses to species that were planted in at least four sites, and we identified the most 'successful' species as those that were recorded in community surveys of at least 50% of these sites (Fig. 1, Table S6). To determine whether there was a phylogenetic signal in this subset of species, we compared the unstandardized MPD and MNTD of 'successful' species to null distributions of MPD and MNTD (999 each) as above. If the MPD or MNTD of the 'successful' species were greater than 97.5% of the random values, then this would indicate that these species were more widely dispersed across the phylogeny than expected by chance; values lower than 97.5% of the random values indicate that these species

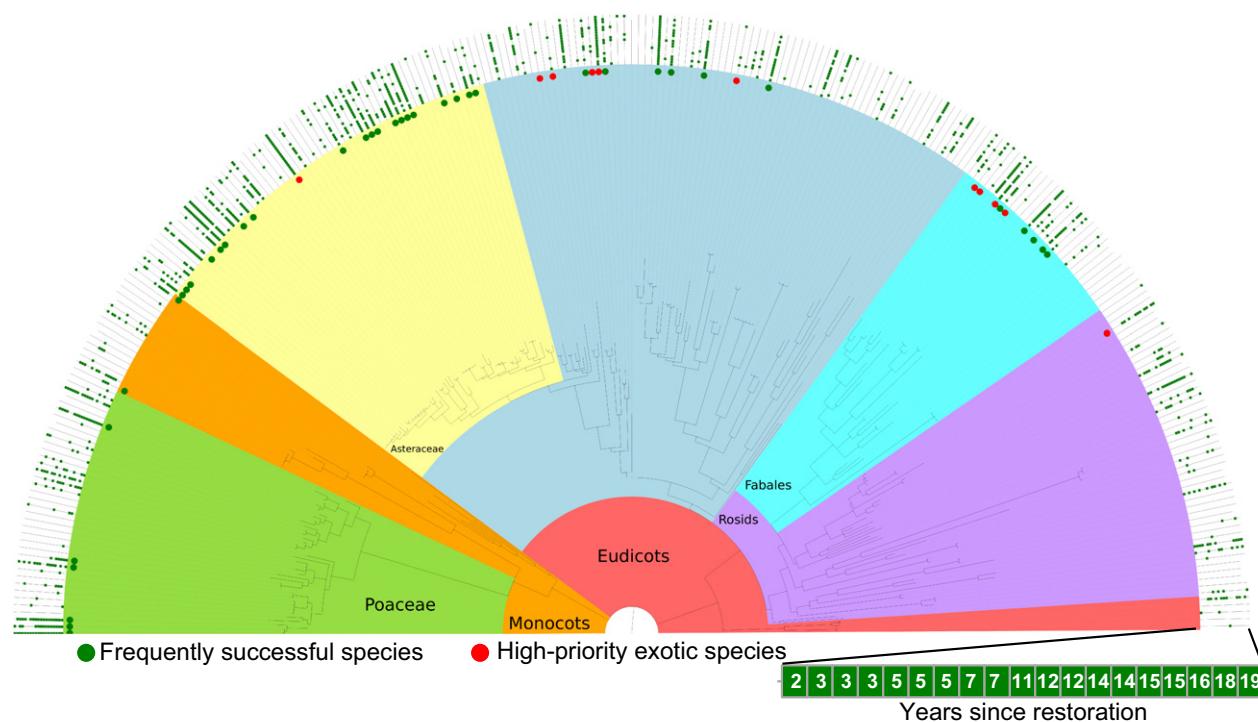


Fig. 1. Majority-rule consensus tree obtained from the Bayesian inference analysis of *rbcL* and *matK* loci from 270 plant species recorded in surveys or included in seed mixes in restoration sites. The arithmetic mean estimate of the marginal likelihoods in this analysis was -73098.93 . Green dots are successful planted species, and red dots are high-priority exotics. Green boxes at the perimeter illustrate the presence of each species in restored sites, arranged by age with younger sites on the inside.

were significantly clustered on the phylogeny and were thus more closely related than expected by chance.

To determine whether seed mixture PD influenced exotic species invasion, we classified species as native or exotic to North America prior to European colonization (based on Swink & Wilhelm 1994). Managers from Nachusa Grasslands rated these species as high or low priority for control during the restoration process; that is, whether or not they actively remove the species through chemical or mechanical methods. Although there were 40 exotic species identified in the surveys, most are not considered threats to the diversity of restoration plantings and are ignored. However, managers identified 11 species as high priority (Table S7). We analysed the number of these high-priority species and total exotic richness using GLMs as described above, treating the MPD or MNTD of the seed mix and age of the site as fixed independent variables. We also analysed the proportion of the total richness at each site that high-priority exotics or all exotics represented using GLMs with binomial error distributions and logit-link function, evaluating site age as an independent variable with a Wald z test. The proportion of total exotics was analysed using quasibinomial distribution to account for overdispersion. We analysed ANPP using GLMs with seed mixture MPD or MNTD and age as fixed independent variables.

Results

COMMUNITY PATTERNS AND SEED MIXTURE EFFECTS

Species richness declined with time since restoration ($t = 2.58$, $P = 0.019$) (Hansen & Gibson 2014) (Fig. 2a), but neither MNTD ($t = 0.84$, $P = 0.413$) nor MPD ($t = 1.48$,

$P = 0.156$) was related to site age (Fig. 2b, c). Across the 17 years of restoration, MPD ($t = 0.69$; $P = 0.505$) and MNTD ($t = 1.89$; $P = 0.080$) of the seed mixture did not show a consistent pattern of change; that is, although the composition of the seed mixture differed from year to year, its PD did not increase or decrease over time. However, seed mixture PD was not correlated with the resulting community PD, and precipitation had no effect (Table 1).

When compared to a null distribution of MPD and MNTD values of these species randomly assigned to tips on the phylogeny, MNTD of 'successful' species was significantly lower than expected by chance (MNTD = 0.118 (vs. null 0.164), $P = 0.028$), indicating that they are phylogenetically clustered. MPD of 'successful' species did not significantly differ from the null mean (MPD = 0.665 (vs. null 0.715), $P = 0.131$).

INVASION RESISTANCE AND PRODUCTIVITY

We tested whether seed mixture PD affected invasion by exotics in general and 11 exotic species ranked as high priority for eradication by managers at the study site. Whether examining the number of species present or their proportion of total species richness, seed mixture MPD and MNTD had no effect on total exotics or high-priority exotics, although exotics proportion tended to increase with restoration age (Table 2). ANPP was also unrelated to seed mixture MPD, but there was a marginally significant trend for it to increase with seed mixture MNTD (Table 2).

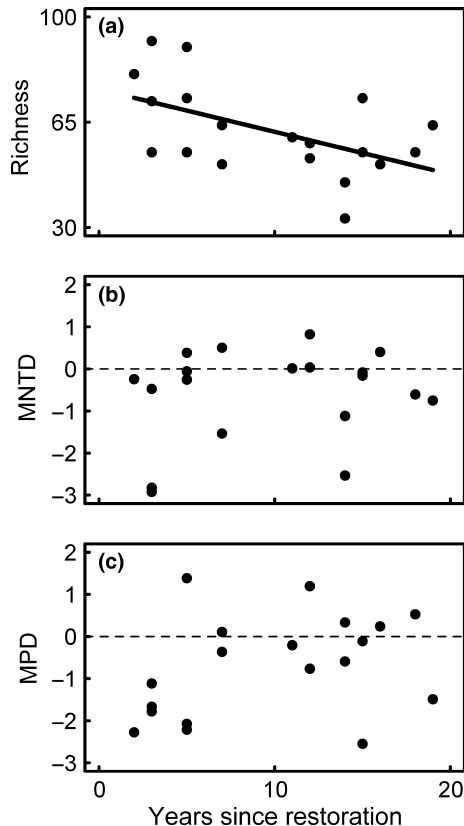


Fig. 2. Relationship between restoration site age and plant community at each site, illustrating that (a) species richness declined as sites aged (adapted from Hansen & Gibson 2014), but (b) mean nearest taxon distance (SES_{MNTD}) and (c) mean pairwise distance (SES_{MPD}), measures of phylogenetic diversity, did not change with site age.

Table 1. Results of generalized linear models analysing the effects of seed mix PD, age of restoration site and mm precipitation in May–August of the first year of growth on plant community MPD and MNTD. The PD metric (MPD or MNTD) used as independent variable in each model was the same metric as in the dependent variable

	Community MPD		Community MNTD	
	Wald <i>t</i>	<i>P</i>	Wald <i>t</i>	<i>P</i>
Seed mix PD	0.87	0.401	0.62	0.547
Summer precipitation	0.77	0.453	0.29	0.778

Discussion

Despite the importance of ecosystem restoration to biodiversity conservation, restoration ecology has largely neglected consideration of the evolutionary history of organisms used when re-establishing natural systems. Phylogenetic patterns of restored communities represent additional criteria for judging the success of restorations given correlations between plant PD and communities' stability, productivity, resistance to invasion and support of higher trophic levels. Here, we show that plant species

richness declines in restored grasslands as the restorations age, yet both MPD and MNTD do not decline, indicating that PD is maintained in the face of local extinctions. MPD tends to reflect deeper branching patterns of a phylogeny, while MNTD describes the redundancy of closely related species closer to branch tips (Webb *et al.* 2002). The patterns we document indicate that these local extinctions (and local colonizations, when they occur) are not biased towards phylogenetically redundant or phylogenetically distinct species. That is, extinction is not more likely for species with or without close relatives in the community, as both these scenarios would be expected to increase MPD or MNTD, respectively. If PD positively correlates with the diversity of functionally important traits in plant communities, as has been hypothesized (Webb *et al.* 2002), then this result suggests that species losses in restored communities may not necessarily lead to reduced ecosystem function.

To determine whether community patterns were driven by initial planting conditions, we examined PD of the seed mixture applied to 16 sites where mixture composition data were available. There were no relationships between seed mixture MPD or MNTD and the resulting plant community, so increased PD of a planted seed mixture did not result in a more phylogenetically diverse community. We further investigated whether environmental conditions in the first year of growth influenced resulting community phylogenetic patterns by including summer precipitation in these models. Although drought might be expected to act as an environmental filter, reducing the likelihood that some plant lineages with lower drought tolerance will become established, there was no relationship between precipitation and community PD. This result agrees with a previous finding that grassland plant population responses to water availability were not phylogenetically conserved (Bennett & Cahill 2013). We also obtained monthly Palmer Drought Severity Index (PDSI) values for the state of Illinois. Substituting summer PDSI for precipitation values, which were highly correlated, still resulted in no significant relationships with resulting community PD (results not shown).

We are confident that the seed mixes planted at the sites contained a sufficient variation in PD to address our research questions. To verify this, we assembled 1000 random hypothetical seed mixes from the total list of species included in all planted seed mixes. Each random mix contained 50 species (mean richness of planted seed mixes used in the study = 49.9). We calculated unstandardized MPD and MNTD (not standardized effect sizes) for each random mix and compared these distributions to the values of the planted seed mixes used at the study sites. MPD of the planted seed mixes ranged from the 1st to 81st percentile of the random mix distribution, and MNTD ranged from below the minimum value to the 80th percentile of the random mix distribution. Thus, although managers at the study site have not taken PD *per se* into account when assembling seed mixes, they have created mixes that are comparable to the variation expected from randomly choosing species.

Table 2. Results of generalized linear models analysing the effects of seed mix PD and age (years since restoration) on the number of high-priority exotic invasive species in the community, the proportion of total community richness these species represent and ANPP

	The number of exotic species				Proportion of Community				ANPP	
	Total exotics		High priority		Total exotics		High priority			
	Wald <i>t</i>	<i>P</i>	Wald <i>t</i>	<i>P</i>	Wald <i>z</i>	<i>P</i>	Wald <i>z</i>	<i>P</i>	Wald <i>t</i>	<i>P</i>
Seed mix MPD	0.35	0.736	0.24	0.812	1.20	0.253	0.32	0.746	0.36	0.722
Age	0.57	0.576	1.19	0.257	2.17	0.050	1.87	0.061	0.76	0.458
Seed mix MNTD	0.80	0.435	1.03	0.322	0.32	0.753	0.50	0.62	2.15	0.051
Age	0.23	0.825	0.61	0.550	1.89	0.082	1.52	0.13	0.23	0.820

There was a significant signal of phylogenetic clustering for the most successful species in the prairie restorations such that species most likely to establish following planting tended to be clustered closer on the phylogeny than expected by chance. Of these 39 species, 20 are in the family Asteraceae, representing 47% of Asteraceae species recorded in restorations. Similarly, six species in Poaceae were successful. Both of these families are prolific seed producers and may be able to establish self-sustaining populations more rapidly than species in many other families. High establishment probability for seeds of these species may limit overall PD if these species, from a limited number of clades, out-compete other unrelated species and dominate the community.

Because the chronosequence approach mimics repeated observations of community composition over time, research approaches like ours may have implications for understanding plant community assembly, where phylogenetic pattern has been proposed as a way to interpret the mechanisms structuring communities. In this view, communities composed of species clustered on a phylogeny (lower PD) indicate habitat filtering that selects for lineages that are adapted to local conditions. Alternatively, when strong competition between close relatives with ecological similarity due to shared ancestry is an important structuring force, the result is more phylogenetically dispersed communities (less clustering, hence higher PD) (Webb *et al.* 2002; Cavender-Bares, Keen & Miles 2006). However, both of these processes rest on assumptions such as phylogenetic niche conservatism (Wiens & Graham 2005) that have been questioned (Araya *et al.* 2012; Gerhold *et al.* 2015) and remain unresolved. We acknowledge that the value of PD information for community ecology theory and for restoration ecology depends in part on such assumptions that are not yet thoroughly understood and that these represent important avenues for future ecological and evolutionary research.

RESTORATION MANAGEMENT IMPLICATIONS

Increased plant community PD has been linked to invasion resistance (Lososová *et al.* 2015), leading to predictions that PD could be a useful tool in restoration management to mitigate the negative effects of invasive

exotics (Hipp *et al.* 2015). We tested whether a more phylogenetically diverse seed mixture led to communities with fewer problematic exotic species, but we found no effects on the richness or prevalence of these invaders. Given that high-priority exotics are specifically targeted for control at the site, the presence of low-priority exotics might better reflect PD effects, but analysis of these remaining species shows that their presence is not related to MPD or MNTD (results not shown). Combined with our finding that PD of resulting restored communities was unaffected by the PD of the seed mixture applied, these results cast doubt onto whether composing seed mixes simply to maximize PD will help to achieve restoration goals of increased diversity and reduced invasion. Instead, careful selection of species based on their phylogenetic relationships with (and trait similarities to) locally problematic invasives may be more effective given evidence that exotic species are less likely to invade local communities with similar species (Carboni *et al.* 2015). There was a trend for seed mixes with higher MNTD to result in greater ANPP, even when controlling for site age. If this pattern is consistent in other restoration projects, it may represent a value of high PD seed mixes as a way to predict ecosystem function in restorations where carbon sequestration through increased primary productivity is a goal.

We propose that managers and restoration practitioners should employ 'phylogenetically informed species selection' (Larkin *et al.* 2015) when planning restoration projects, but in a more nuanced way than simply maximizing total seed mixture PD. Rather, combining close native relatives should be avoided if one species is likely to be competitively excluded by a congener. Further, species that are susceptible to exclusion should be identified for establishment in target areas, separate from competitors, where they will be most likely to succeed. This approach may avoid the costs of actively removing a native species to allow the establishment of a more desirable relative, as is sometimes done (Carey *et al.* 2012). At deeper phylogenetic levels, targeting underrepresented lineages in seed collection may help increase overall PD if these species are likely to establish and less susceptible to exclusion.

The primary limitation to high PD (and higher species richness in general) may be the overall low success rate of

many planted species. In all but one site, half or fewer of the planted species were recorded in surveys, indicating that most planted species failed to establish, either at early seedling stages or later due to competition. Members of Asteraceae and Poaceae, which tend to have high establishment success rates here and in other projects (Schramm 1990), are likely candidates for competitively dominant species. Reduced seeding densities of these families could increase establishment rates for members of other plant clades. At a finer taxonomic level, and complementing the above recommendation to identify species susceptible to exclusion, recognizing and limiting the most dominant species within these groups would be an effective way to maintain higher-level phylogenetic community structure while increasing it at the within-family or within-genus level. For example, in *Symphyotrichum* (Asteraceae), eight different species were planted in a variety of combinations, but after the first three growing seasons, two species (*S. ericoides* and *S. laeve*) tended to outlast any congeners planted. Eliminating these two species from seed mixes (or greatly reducing their seeding density) might achieve this goal. However, we acknowledge that seed mix composition is also constrained by availability, that species which achieve high densities often are the most readily available species, and that rapid establishment of native species is often necessary to minimize exotic invasions.

These recommendations to increase the PD of restorations will require a more thorough understanding of the impact of phylogenetic relatedness on species interactions. Ecologists will need to develop a robust predictive framework to identify species that are more or less susceptible to exclusion (Hipp *et al.* 2015). Recent advances in coexistence theory may help to identify the trait combinations that lead to competitive exclusion or coexistence (Godoy, Kraft & Levine 2014; Kraft, Godoy & Levine 2015; Kraft *et al.* 2015). Examining the phylogenetic signals of these traits and of average fitness differences between species could allow predictions for when phylogenetically clustered or dispersed species combinations are more likely to establish successfully in restorations.

Ecological restoration brings significant hope that conservation practitioners can repair damaged ecosystems and stem the biodiversity crisis. However, many restoration projects result in lower richness or functions than undisturbed reference systems (Benayas *et al.* 2009; Moreno-Mateos *et al.* 2012), resulting in incomplete recovery and ecosystems that fail to maximize services vital to humanity. Establishing combinations of species that maximize the evolutionary diversity of restored communities may enhance functional diversity in ways that lead to greater ecosystem service delivery, an essential goal of ecosystem restoration. There are calls for PD to become an important consideration in ecosystem conservation (Winter, Devictor & Schweiger 2013; Hipp *et al.* 2015; Shooner, Chisholm & Davies 2015). In a similar vein, a major goal for restoration ecologists should be to enlist phylogenetic and functional diversity to restore ecosystem function in real-world

settings, scaling up from the carefully controlled plot experiments that have been performed in the past.

Acknowledgements

We are grateful to W. Kleiman, C. Considine and The Nature Conservancy for providing logistical support of this project and O. Schmitz and two anonymous reviewers for providing helpful comments on the manuscript. We thank B. Bailey, J. DiGiovanni, C. Jaeger and L. Reinke for laboratory assistance. Funding was provided by The Nature Conservancy, Northern Illinois University and Southern Illinois University Carbondale.

Data accessibility

Phylogenetic data: TreeBASE study accession no. S18945.

Plant community data and site descriptions: Dryad Digital Repository doi:10.5061/dryad.5m30d (Barber *et al.* 2016).

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Received 21 October 2015; accepted 26 February 2016

Handling Editor: Marc Cadotte

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Restoration site characteristics.

Table S2. Species in seed mixture for 16 of the 19 study sites.

Table S3. GenBank accession numbers for *rbcl*.

Table S4. GenBank accession numbers for *matK*.

Table S5. Species missing from phylogeny.

Table S6. ‘Successful’ species planted in restorations.

Table S7. High-priority exotic species.