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Taxon sampling effects on the quantification and comparison of community phylogenetic diversity

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Abstract

Ecologists are increasingly making use of molecular phylogenies, especially in the fields of community ecology and conservation. However, these phylogenies are often used without full appreciation of their underlying assumptions and uncertainties. A frequent practice in ecological studies is inferring a phylogeny with molecular data from taxa only within the community of interest. These "inferred community phylogenies" are inherently biased in their taxon sampling. Despite the importance of comprehensive sampling in constructing phylogenies, the implications of using inferred community phylogenies in ecological studies have not been examined. Here, we evaluate how taxon sampling affects the quantification and comparison of community phylogenetic diversity using both simulated and empirical data sets. We demonstrate that inferred community trees greatly underestimate phylogenetic diversity and that the probability of incorrectly ranking community diversity can reach up to 25%, depending on the dating methods employed. We argue that to reach reliable conclusions, ecological studies must improve their taxon sampling and generate the best phylogeny possible.

KEYWORDS
community ecology, community phylogeny, divergence time estimates, phylogenetic distance, phylogenetic diversity, taxon sampling

1 | INTRODUCTION

Over 150 years ago, Darwin (1859) noted the connection between the evolutionary relationships of taxa and community ecology. In the last few decades, the conceptual advantages of incorporating phylogenetics and ecology have been rediscovered and reimagined (Brooks & Mclennan, 1991; Losos, 1996; Webb, 2000). Tremendous advances in computational methods as well as the increased availability of phylogenetic data have led to the rapid expansion of efforts applying information about the evolutionary history and relationships of species to questions of community assembly and diversity (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Webb, Ackerly, McPeek, & Donoghue, 2002). Such approaches have allowed ecologists to link short-term local processes to continental and global processes that occur over deep evolutionary timescales, assessing the relative influence of niche-related, neutral and historical processes on the assembly of communities and the coexistence of species (Cavender-Bares & Wilczek, 2003; Cavender-Bares et al., 2009; Emerson & Gillespie, 2008; Park & Potter, 2013; Vamosi, Heard, Vamosi, & Webb, 2009; Webb et al., 2002). However, concerns about the limitations of these approaches have been voiced as well (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Losos, 2011).

Incorporating inherently spatial (ecological) and historical (evolutionary) fields necessitates careful consideration of the requirements of both disciplines. The importance of comprehensive, balanced sampling in generating reliable phylogenies has been widely supported among systematists. The inclusion of species representing the broad taxonomic, biogeographical and morphological diversity of a clade improves phylogenetic reconstruction by reducing the effects of long branch attraction and other topological anomalies such as stochastic error and poorly resolved trees with low support (Baurain, Brinkmann, & Philippe, 2007; Heath, Hedtke, & Hillis, 2008; Hedtke,

Townsend, & Hillis, 2006; Hillis, Pollock, McGuire, & Zwickl, 2003; Parfrey et al., 2010; Pick et al., 2010; Yi, Dunthorn, Song, & Stoeck, 2010; Zwickl & Hillis, 2002). Supertree methods, which prune and graft taxa from existing phylogenetic trees, can be used to construct community phylogenies, ameliorating concerns of biased taxon sampling to some degree (Webb and Donoghue, 2005). However, unless the available reference trees comprise all taxa of interest, which is often not the case for diverse ecological communities (Erickson et al., 2014), the relationships of many species can only be inferred at higher taxonomic levels where relationships are completely resolved (Kress et al., 2009), resulting in the loss of information towards the tips of the phylogeny. Furthermore, a supertree assembled from separate phylogenies is unlikely to contain precise information on evolutionary distances (i.e., branch lengths). As the use of phylogenies in community ecology is dependent upon these distances, branch lengths must be inferred as accurately as possible (Erickson et al., 2014). Not only does undersampling negatively impact the accurate reconstruction of the topology of phylogenetic trees, it also affects divergence time estimations (but see Zheng & Wiens, 2015). It has been shown that sparser taxon sampling leads to generally underestimated node ages (Linder, Hardy, & Rutschmann, 2005), and node age estimates become significantly more precise (i.e., smaller credible intervals) as taxonomic sampling increases (Soares & Schrago, 2012).

Along these lines, a common practice in community ecological studies of particular concern is that of inferring a phylogeny with data from only the members of the site or species pool of interest (e.g., Godoy, Kraft, & Levine, 2014; Li et al., 2015; Pellissier et al., 2013). Coexisting species have rarely evolved in sympatry, as species distributions shift over time (Coyne & Orr, 1989, 1997). Therefore, while spatial assemblies of species can constitute ecological/functional units, in most cases, these communities are nonmonophyletic assemblages of taxa and hence not evolutionary units. On the other hand, the discovery and classification of monophyletic groups are the crux of phylogenetics, where evidence for common ancestry is sought regardless of where species may (co-) occur. Thus, community phylogenies inferred from only community members (hereafter, "inferred community phylogenies/trees") are inherently biased in their sampling. For instance, Li et al. (2015) inferred a community phylogeny spanning the angiosperms with 19 taxa from 11 families, missing any representatives from several important orders such as Fagales, Rosales and Saxifragales. On an even larger, continental scale, Thuiller et al. (2011) inferred the phylogenetic relationships of all European plants from a tree missing major clades including monocotyledons, legumes and sunflowers, casting serious doubts on their conclusions (Davis, Schaefer, Ruhfel, Donoghue, & Edwards, 2014). While this issue seems especially prevalent in studies of plant communities (e.g., Barber et al., 2017; Bhaskar, Porder, Balvanera, & Edwards, 2016; Condit, Engelbrecht, Pino, Pérez, & Turner, 2013; Funk & Wolf, 2016; Godoy et al., 2014; Kress et al., 2009; Li et al., 2015; Lososová et al., 2016; Marx, Giblin, Dunwiddie, & Tank, 2016; Matos et al., 2017; Mi et al., 2016; Montesinos-Navarro, Verdú, Querejeta, & Valiente-Banuet, 2017; Navarro-Cano et al., 2016; Pellissier et al., 2013; Pistón, Schöb, Armas, Prieto, & Pugnaire, 2016; Staab et al., 2016; Xu et al., 2016), it is present in animal studies as well (e.g., Arnan, Cerdá, & Retana, 2017). To determine how prevalent this practice is currently, we surveyed the scientific literature of 2017 using the Boolean search term "community AND (phylogenetics OR phylogeny OR tree)." We included studies that used phylogenetic data (as opposed to taxonomic ranks) and excluded reviews, posters, books, conference abstracts or other non-peer-reviewed articles. The search yielded 71 studies that met our inclusion criteria. An examination of this community phylogenetics literature revealed that in 44% of studies, researchers built their own phylogenies from molecular data, and among these, 53% used inferred community phylogenies (Table S1). Likewise, over half (52%) of the studies that utilized previously published phylogenies either used inferred community phylogenies or inferred divergence times only with the taxa of interest. As Harvey and Pagel (1991) accentuated, "...biologists should be aware of the fact that they may well be working with the wrong tree!" and consider the uncertainty in inferred phylogenetic relationships and divergence times (Smith, 2009). The results of an ecological study based on a particular phylogenetic tree could be overturned if re-examination of the group yields different phylogenies (Huelsenbeck, Rannala, & Masly, 2000). Indeed, it has been shown that low phylogenetic resolution can negatively impact the quantification of phylogenetic diversity and dispersion of communities (Swenson, 2009), as well as estimations of phylogenetic conservatism (Davies, Kraft, Salamin, & Wolkovich, 2012).

Community phylogenetic studies are often dependent upon the correct calculation and comparison of the phylogenetic diversity of and/or among different communities. Metrics commonly applied to describe phylogenetic community patterns include Faith's PD (Faith, 1992), mean phylogenetic distance (MPD), mean nearest neighbour (taxon) distance (MNND/MNTD) and their standardized derivatives, such as net relatedness index (NRI) and nearest taxon index (NTI) (Webb et al., 2002). These metrics have been used in a wide range of contexts from investigations of the biological invasion process showing that close relatives make bad neighbours (Park & Potter, 2015b), to demonstrating that phylogenetic diversity promotes ecosystem stability (Cadotte, Dinnage, & Tilman, 2012). Although these metrics have been well reviewed and become standard for community studies (Tucker et al., 2016), there has been little investigation into how these metrics are affected by the properties of the phylogenies they are based upon (Boyle & Adamowicz, 2015).

Given that node age estimates tend to be underestimated in sparsely sampled phylogenies (Linder et al., 2005), we expect that metrics of phylogenetic diversity will be underestimated in inferred community phylogenies. However, we hypothesize that this underestimation is not likely to be constant across the tree, as subclades will have differing degrees of undersampling. This can lead to different degrees of inaccuracy when calculating and comparing the phylogenetic diversity of communities on inferred community phylogenies, depending on the characteristics of the communities. For instance, we might expect that node age estimates, and comparisons of

phylogenetic diversity on inferred community phylogenies, would be less accurate between communities clustered distantly from each other on the tree of life than between communities that are overdispersed and share close lineages with each other, because the taxon sampling of the latter is likely to be more even for the clade that comprises members of all communities. Furthermore, we may expect these biases to be compounded in metrics that consider multiple branches (e.g., MPD).

Here, focusing on divergence time estimations, we evaluate the problems that can arise when using undersampled inferred community phylogenies to address ecological questions and propose phylogenetically sound approaches to community ecology using both simulated and empirical data. We examine how accurately inferred community phylogenies calculate and contrast phylogenetic diversity of and among different communities, focusing on PD, MPD and MNND. In lieu of commonly performed community phylogenetic analyses, we investigate the degree to which community trees inferred from limited taxon sampling can (i) correctly determine (rank) which communities are more phylogenetically diverse than others (i.e., alpha diversity comparisons) and (ii) accurately deduce which two of three communities are more closely related to each other (i.e., beta diversity comparisons). We demonstrate that even in ideal situations, incomplete, unbalanced taxon sampling can lead to spurious conclusions regarding phylogenetic community patterns.

2 | METHODS

To assess the baseline error in community diversity comparisons that can occur when using phylogenies generated with limited taxon sampling, we created idealized phylogenetic situations using both empirical and simulated DNA sequences. The structure of our data and workflow is detailed below and outlined in Figure 1. Here, we do not attempt to test the accuracy of different dating methods. Rather, we examine how the undersampling of taxa can bias the phylogenetic diversity calculations and comparisons across commonly used metrics and tree dating methods.

2.1 | Generating species pools

Community phylogenetics studies are sometimes focused on relatively closely related groups of taxa (e.g., Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004), but can also involve taxa separated for over 100 million years (myr) (e.g., Schaefer, Hardy, Silva, Barraclough, & Savolainen, 2011). Thus, to encapsulate the scales observed in the literature, we assembled phylogenetic data sets of four well-supported clades, spanning less than 50 myr (sunflowers [family Asteraceae] and dodder [genus *Cuscuta*]) to over 100 myr (grasses and relatives [order Poales] and ferns [subclass Polypodiidae]). These taxa encompass temporal and phylogenetic diversity comparable to those examined by many ecological studies (see following sections for details of phylogenetic analyses). Within these clades, we generated unique series of communities following Cavender-Bares and Wilczek (2003), where each of the communities in these series is either phylogenetically clustered or overdispersed (Figure 2). Phylogenetically clustered communities can arise as the result of strong environmental filtering, whereas more overdispersed community structures may be the result of competitive exclusion among closely related, functionally similar taxa (Cavender-Bares & Wilczek, 2003). Three communities of 30 taxa each (five for *Cuscuta*) were either drawn from (i) mutually exclusive clades so that members of a community always share a more recent common ancestor with each other than with taxa in other communities (e.g., type A: phylogenetic clustering) or (ii) from nonexclusive clades that also contain members of other communities (e.g., type D: overdispersion). Overdispersed communities were assembled so that some members of the community share a more recent common ancestor with members of another community. Phylogenetically clustered communities were generated by identifying exclusive monophyletic groups comprising more than 30 taxa (5 for *Cuscuta*) then drawing species randomly within for a single community. Overdispersed communities were generated by randomly sampling members for three communities from all species across the full phylogeny, then screening for communities that belonged to clades that included members of other communities. We then sampled 600 sets of communities evenly across a distribution of phylogenetic gamma diversity to ensure that communities with a wide range of community alpha and beta diversity were tested. Together, these sets of three communities represent regional species pools of 90 species (15 for *Cuscuta*) across the range of possible taxon dispersion on the fully sampled phylogenies of each group. Thus, all species in the species pool belong to a one of the three communities. A total of 2,400 unique sets of three communities (species pools) were generated for each of the four scenarios depicted in Figure 2. The large amount of communities generated (9,600 in total) allowed us to examine a wide range of possible community phylogeny topologies. To reduce the number of variables that may influence the calculation and comparison of phylogenetic diversity on community trees, we kept the size and number of communities constant throughout our study.

2.2 | Empirical phylogenetic data

We used the program PHLAWD (Smith, Beaulieu, & Donoghue, 2009) to harvest data from GenBank Release 207.0, selecting taxa to represent all major lineages of each of the four selected clades. We downloaded gene sequences of maturase K (*matK*), the internal transcribed spacer 1, 5.8S rRNA gene and internal transcribed spacer 2 region (ITS) for Asteraceae, ITS, 26S ribosomal RNA gene (26S), and ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcL*) for *Cuscuta*, *matK* and NADH dehydrogenase subunit F (*ndhF*) for Poales, and *rbcL* and ribosomal protein S4 (*rps4*) for Polypodiidae (see Table S2). Sequences of each gene region were aligned separately with MAFFT-GINSI v7.220 (Katoh & Standley, 2013) and then concatenated. To reduce error and bias in taxon placement and branch length calculations, missing data were minimized, with only a small portion of taxa in the genus *Cuscuta* lacking any gene regions

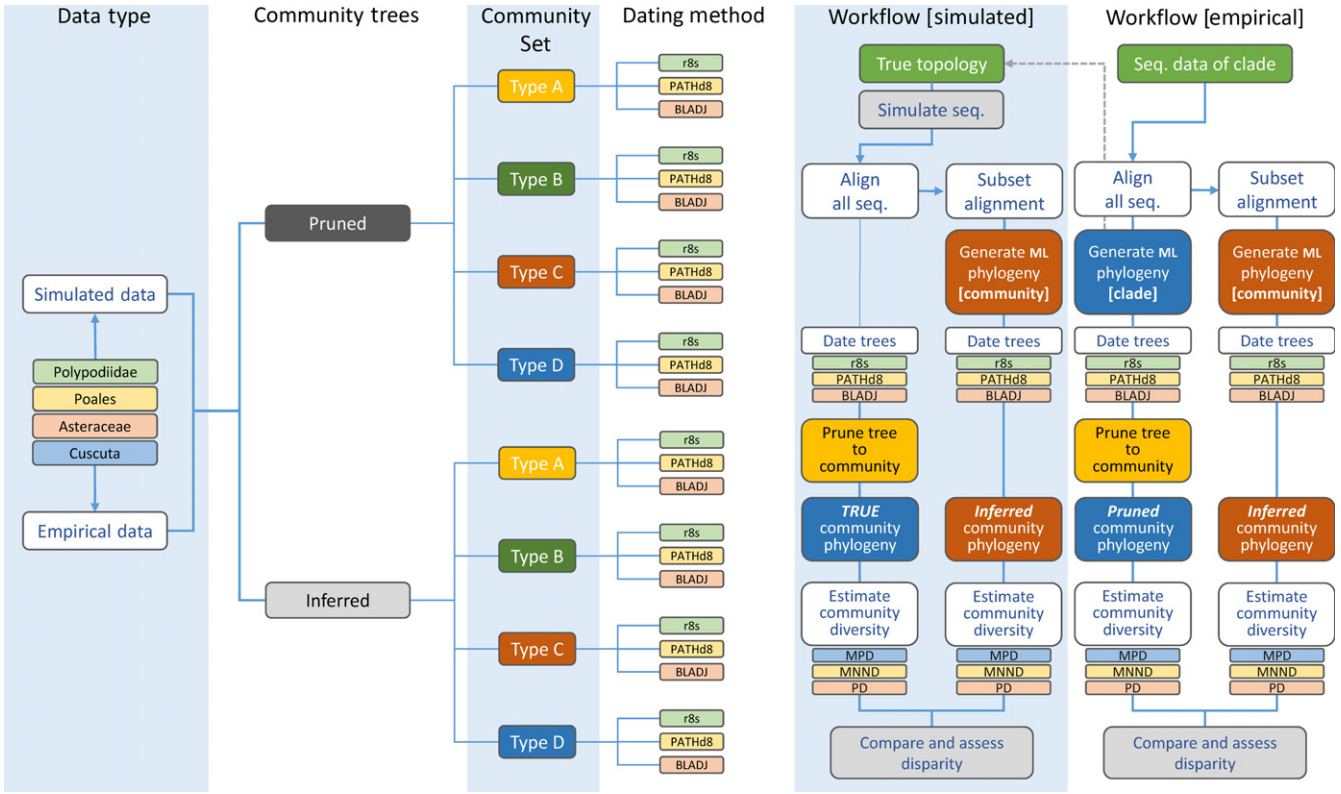

FIGURE 1 Workflow and structure of empirical and simulated data sets used to assess community phylogeny error in phylogenetic diversity estimations and comparisons. The dendogram depicts the experimental design of our data. Workflows for simulated and empirical data are depicted in the right two panels. In the simulated workflow, pruned community phylogenies represent the true community phylogeny [Colour figure can be viewed at wileyonlinelibrary.com]

in the alignment (Table S2). The lengths of the alignments were as follows: 1,441 taxa for Asteraceae (2,808 bp), 177 for *Cuscuta* (2,969 bp), 892 for Poales (3,801 bp) and 1,220 for Polypodiidae (1,879 bp). These alignments were used to construct fully sampled maximum-likelihood (ML) phylogenies of each clade using RAXML v8.1.3 (Stamatakis, 2014) with a GTR+Γ model specified for each gene region ("-m GTRGAMMAX -u -f d -N 3").

The fully sampled ML trees of each clade were dated with three commonly used methods in community phylogenetics studies, including local substitution rate smoothing with PATHD8 v1.0 (Britton, Anderson, Jacquet, Lundqvist, & Bremer, 2007), a penalized likelihood approach utilizing R8S v1.71 (Sanderson, 2003), and BLADJ as implemented in PHYLOCOM v4.2 (Webb, 2000; Webb, Ackerly, & Kembel, 2008). A single calibration point at the root node of each tree was enforced as a fixed age: 50 myr for Asteraceae (Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández, 2015; Wikström, Kainulainen, Razafimandimbison, Smedmark, & Bremer, 2015), 68 myr for *Cuscuta* (Dillon, Tu, Xie, Quipuscoa Silvestre, & Wen, 2009), 105 myr for Poales (Hertweck et al., 2015; Magallón et al., 2015) and 330 myr for Polypodiidae (Rothfels et al., 2015; Zhong, Fong, Collins, McLenachan, & Penny, 2014). This was made to keep the number of nodes between the calibration point and tips stable, as the number of nodes between calibration points can influence divergence time estimations (Zheng & Wiens, 2015). The dated phylogenies of each clade were pruned to only include taxa occurring within each of the 600 species pools (pruned community phylogenies) for downstream analyses (see following section for species pool generation details).

We also constructed separate ML community phylogenies using only sequences of taxa present in each species pool with parameters identical to those used to construct the fully sampled master phylogenies above. Topologies were held to be constant with the fully sampled phylogenies to eliminate possible errors in phylogeny inference, which can differ depending on the reconstruction method used. These inferred community trees were also dated as above. Thus, our downstream analyses evaluate the calculation and comparison of phylogenetic diversity on community phylogenies pruned from well sampled, dated, phylogenies of each clade versus community phylogenies inferred and calibrated with only taxa occurring in the species pool (Figure 1).

We calculated the phylogenetic diversity of, and among, the three communities within each species pool on all pruned and inferred community phylogenies separately, represented by three commonly used metrics, PD, MPD and MNND (MNTD). PD represents the sum of all branch lengths connecting species of interest; MPD is the mean branch length between each pair of species in the focal set of taxa, and MNND is the mean branch length between

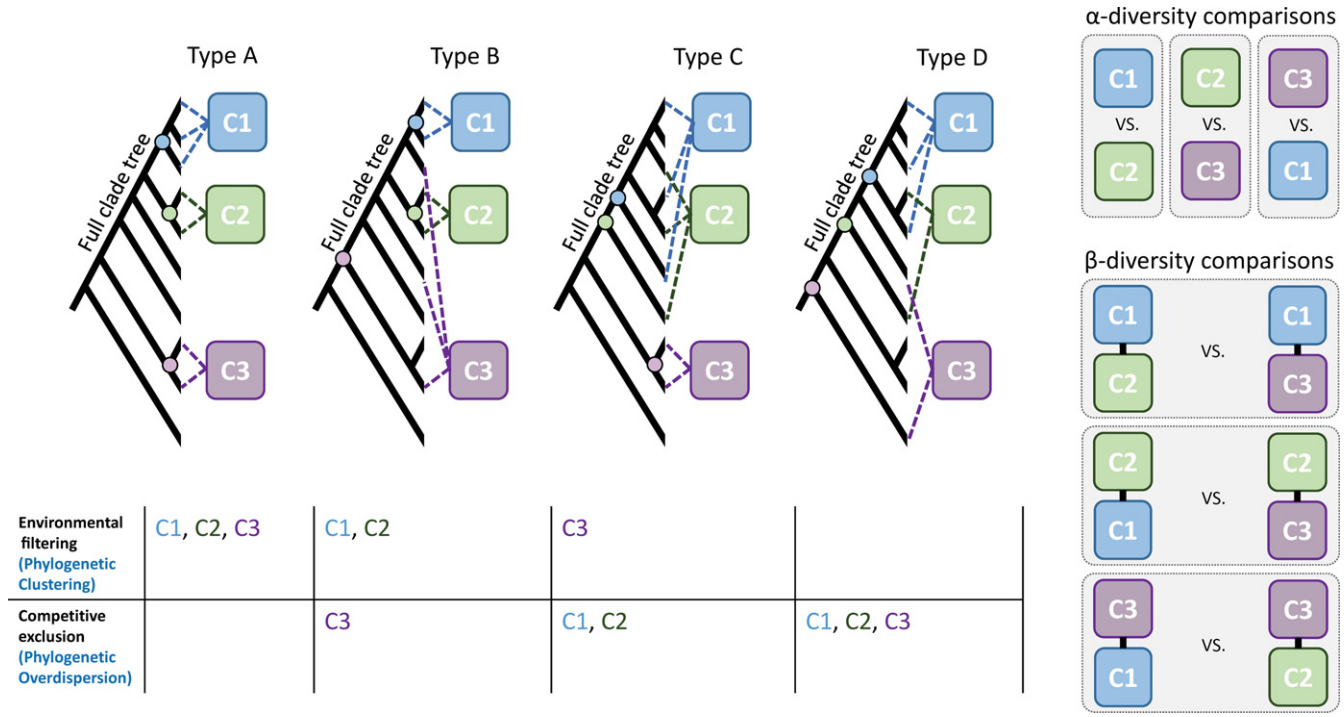

FIGURE 2 Community generation scheme and comparisons. Sets of three communities were generated for every data set, each representing either environmental filtering or competitive exclusion. Trees represent fully sampled phylogenies of monophyletic groups (clades). C1, C2 and C3 represent ecological communities, and their members are indicated with dotted lines. Coloured dots indicate the most recent common ancestor of each community. Phylogenetically clustered communities have mutually exclusive common ancestors, whereas overdispersed communities do not. The right panel illustrates the types of community phylogenetic diversity comparisons made. Alpha diversity comparisons rank whether the members of one community represent more phylogenetic diversity than do the members of another. Beta diversity comparisons determine which community is more closely related to the focal community [Colour figure can be viewed at wileyonlinelibrary.com]

each species and its closest relative in the group of interest. MPD and MNND values were calculated for each community (alpha diversity) and between communities (beta diversity). Beta MPD is calculated as the mean for all pairwise comparisons of PD between the taxa of two different communities, and beta MNND among nearest neighbour pairs of taxa in different communities (Webb et al., 2002). While beta PD indices have been developed as well (Cardoso, Rigal, & Carvalho, 2015; Cardoso et al., 2014), they have been less commonly used in community ecology, and thus, PD was only calculated as an alpha diversity metric. We then determined whether the communities significantly differed in terms of these metrics by comparing the 95% highest posterior density intervals of each diversity measure (Figure 2). Pairwise comparisons of alpha diversity were made to determine whether a community is significantly more phylogenetically diverse than the other (e.g., PD of community 1 > PD of community 2). Comparisons of beta diversity were conducted to determine whether a focal community is more closely related to one community over another (e.g., MPD between communities 1 and 2 > MPD between communities 1 and 3). We compared the results of inferred community phylogenies with those from pruned community phylogenies and quantified their discrepancies as error. While pruned community phylogenies based on empirical sequence data do not necessarily represent the true evolutionary relationships among community members, they are likely to be more accurate, as better taxon sampling has been shown to increase the accuracy of phylogenies (Zwickl & Hillis, 2002).

2.3 | Simulated phylogenetic data

To create ideal simulated data sets directly comparable to our empirical ones, we used the best-scoring ML phylogeny inferred for each clade of taxa above to represent the true clade phylogeny. We then used these optimal ML topologies to simulate DNA sequences of 3,000 bp using SEQ-GEN v1.3.3 (Rambaut & Grassly, 1997) under the JC69 model (Jukes & Cantor, 1969) of nucleotide evolution to minimize possible convergence and homoplasy. No gaps or missing data were introduced. We chose to simulate DNA sequences based on phylogenies inferred from real molecular data over directly simulating topologies. While the latter approach would allow better exploration of tree space, it does not account for errors and inconsistencies in phylogenetic reconstruction and dating. More importantly, simulated topologies will have the exact same branch lengths regardless of taxon sampling, rendering our investigations into how undersampling affects the calculation and comparison of phylogenetic diversity metrics difficult. Therefore, our approach

ensures that the topologies we generate, and the discrepancies we observe, are as realistic as possible.

These simulated sequences were aligned and used to calibrate the true clade phylogeny, following the same methods used for our empirical data set. As with our empirical approach, the full sampled, dated, true clade phylogenies were pruned to include only the taxa present in the species pools. In this case, these pruned community phylogenies represent the "true community phylogeny." Again, we generated inferred community phylogenies with alignments of simulated sequence data only containing taxa within each species pool. Calculations and comparisons of phylogenetic diversity metrics were carried out identically with our empirical data as described above.

2.4 | Statistical analyses

We used generalized linear models to separately analyse simulated and empirical data. To model the accuracy of community diversity, we used an ordinary least squares estimator. To model the probability of incorrectly ranking phylogenetic diversity, we used logistic regression with various predictors (model specifications are provided in Table S3). The estimated predicted probability of error with 95% confidence interval is reported. Model goodness of fit was assessed using an omnibus *F* test (for linear models) or the Hosmer–Lemeshow chi-squared test (for nonlinear models), with significance of individual estimates determined via two-sided *F* tests or Wald-tests with an alpha level of 0.05 (see Table S4). To avoid inflating the chance of obtaining false-positive results (Type I errors) above the conventional 5%, we corrected *p*-values for multiple comparisons within a family of tests using the sequential Bonferroni method (Holm, 1979). Analyses were also repeated on a subset of groups that did not have any missing data in their alignments. All analyses were performed using R v3.3.2 (R Core Team, 2016), and replication scripts and data are available in a Zenodo repository (Park, Worthington, & Xi, 2017).

3 | RESULTS

In our simulated data set, inferred community trees tended to greatly underestimate community phylogenetic diversity compared to pruned community trees (Figure 3; alpha and beta diversity $p<.0001$). On average, community trees calibrated with BLADJ exhibited the highest probability of error, whereas those calibrated with PATHd8 exhibited the lowest (Figure 4). The nature (type) of these errors varied greatly across diversity metrics, but was similar across simulated and empirical data (see Fig. S1). The proportion of sign errors (type S) was highest for PD ($p<.0001$), for which it comprised over two-thirds of all errors.

In terms of community type, discrepancies between the inferred community trees and the pruned (true) community phylogenies in alpha diversity comparisons were most common when environmental filtering was present in all communities (type A; $p<.0001$ for all pairwise community type comparisons for alpha diversity; Figure 4). The

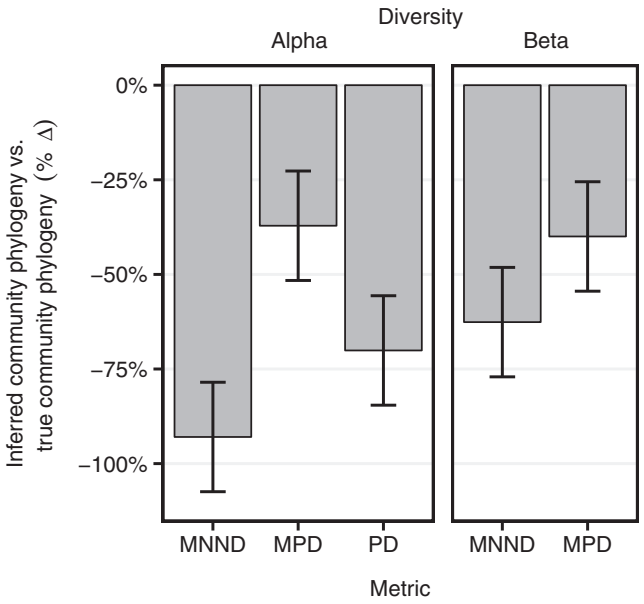

FIGURE 3 Accuracy of diversity estimation on inferred community phylogenies, using simulated data. Bars represent the proportion of departure from the true values calculated from the true community phylogeny. Error bars denote 95% confidence intervals

probability of error in alpha diversity comparisons was highest for trees calibrated using BLADJ for both simulated and empirical alignments ($p<.0001$ for all pairwise dating method comparisons for alpha diversity; Figure 4). The pattern for beta diversity comparisons was less clear (only A–C and B–C comparisons were statistically significant, $p<.0001$; Figure 4). However, error rates were lowest in the absence of environmental filtering (type D) for all diversity metrics. Trees dated with PATHd8 were the least sensitive to incomplete sampling of the clade. Comparisons of MNND were the least affected by incomplete sampling for ranking alpha diversity ($p<.0001$). There was no significant difference between the error rates in comparisons of beta diversity metrics ($p=.93$).

The probability of incorrect community diversity comparisons decreased with increased phylogenetic diversity of the species pool from which the communities were selected (Figs 5, S2). In general, relationships were strongest when communities were confined to exclusive clades (type A) and became weaker in more overdispersed communities. Alpha diversity comparisons were more sensitive to increases in species pool diversity, and MNND comparisons were the most responsive among them.

4 | DISCUSSION

We demonstrate that using inferred community phylogenies derived from incomplete taxon sampling can bias estimations and comparisons of phylogenetic diversity. Overall, similar patterns were observed for both empirical and simulated data, although error rates were slightly higher for empirical analyses. While our analyses

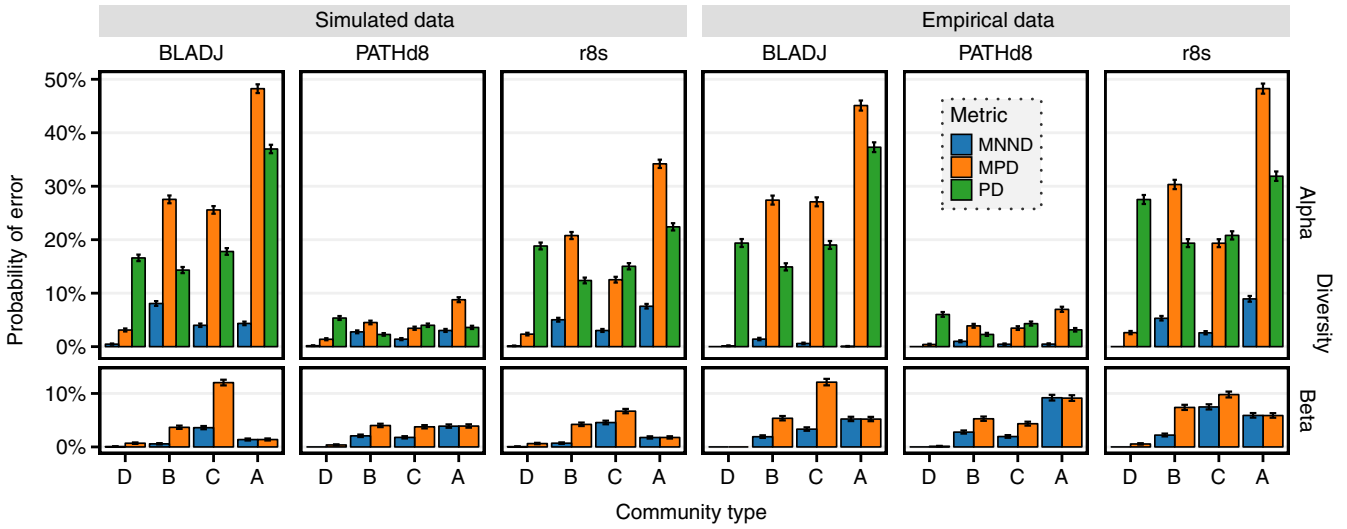

FIGURE 4 Discrepancy between inferred community phylogenies and the true community phylogeny (simulated data) or pruned community phylogeny (empirical data) in phylogenetic diversity rankings by community type. Bars represent the probability of error. Error bars denote 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

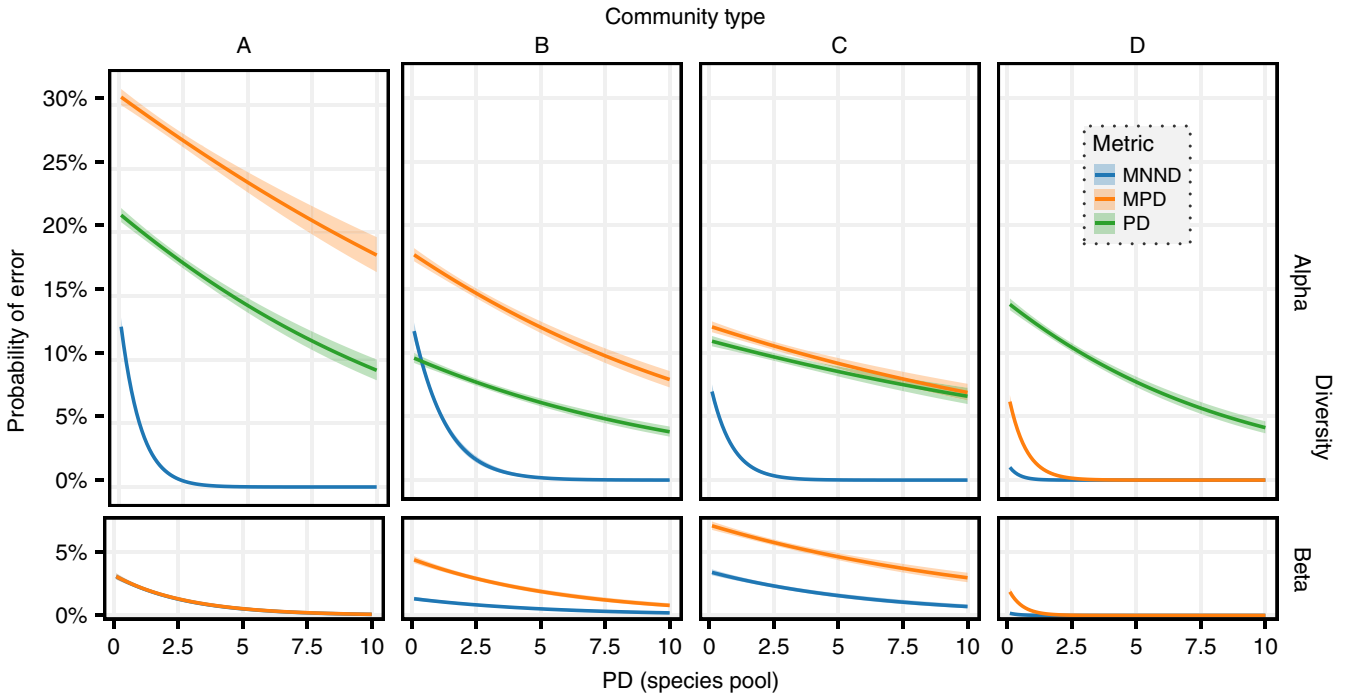

FIGURE 5 Correlations between the phylogenetic diversity of the species pool and levels of discrepancy among inferred community trees and the true community phylogeny in diversity rankings. Lines represent predicted marginal means for the probability of error. Error ribbons denote 95% confidence intervals. Phylogenetic diversity (PD) is expressed in thousands of millions of years [Colour figure can be viewed at wileyonlinelibrary.com]

focused on three basic metrics of alpha and beta phylogenetic diversity, the calculation of these indices is not only related to more complex assessments of phylodiversity, but evaluations of phylogenetic signal, clustering and overdispersion as well. As phylogenetic branch lengths are often assumed to reflect species' functional and ecological similarities, the interpretation of phylogenetic diversity and community structure depends critically upon these estimates (Davies et al., 2012). We observed complex patterns in the biases and errors that can occur when using phylogenetic diversity metrics derived from inferred community phylogenies, but some common themes and predictable differences emerged, which we discuss in detail below.

4.1 | Inferred community phylogenies underestimate phylogenetic diversity

Inferred community trees tended to greatly underestimate both alpha and beta phylogenetic diversity. This corroborates previous findings that undersampling taxa leads to the underestimation of divergence times (Linder et al., 2005; Schulte, 2013). The underestimation of phylogenetic diversity was most pronounced for measurements of MNND. While PD and MPD incorporate the ages of both shallow and deeper nodes in their calculation, as MNND represents the average distance between the closest relatives in a community, it reflects the ages of mostly shallow nodes that connect community members. Hence, the comparatively greater underestimation of MNND suggests that the underestimation of node ages tends to be more severe towards the tips of inferred community phylogenies. Indeed, it has been shown that the influence of taxon sampling on the precision of divergence time estimates is less pronounced in deeper nodes (Soares & Schrago, 2012). Such underestimation of divergence times and phylogenetic relatedness can have consequences for assessments of phylogenetic signal, biodiversity and conservation planning.

4.2 | Community phylogenies incorrectly rank phylogenetic diversity

Ecologists are often interested in the (relative) phylogenetic structure of communities and their drivers, but not the absolute values of phylogenetic distance or diversity. For instance, for questions of relative diversity such as whether certain communities are more diverse than others (Martin, 2002), or if invasive species are more closely related to native species than noninvasive introduced species are (Park & Potter, 2015a), the underestimation of diversity metrics may be less of a problem, as long as the underestimation is even across branches. However, we find that inferred community trees often fail to correctly rank the alpha diversity of, and beta diversity among, communities. The error rate was highest (up to 50%) for inferred community trees dated with BLADJ. This is especially concerning, as BLADJ has become an increasingly popular dating algorithm in ecological studies due to its ease of use. Furthermore, BLADJ is often used in conjunction with trees generated via Phylomatic, which attaches congeners on a collapsed, polytomous genus node if an input taxon is not represented on the backbone phylogeny (Webb and Donoghue, 2005). The resulting lack of resolution can further confound the estimation and comparison phylogenetic diversity. Such high error rates are likely due to the way BLADJ evenly distributes time across nodes between calibration points and/or tips. Thus, sparsely sampled community trees calibrated with BLADJ can display vastly different distributions of divergence times compared to trees with better taxon sampling that have additional nodes that break long branches. The error rate of community trees dated with r8s was greater than that of trees dated with PATHd8, despite the fact that r8s generally produces more accurate divergence time estimates than PATHd8 when fixed age nodes are close to the root as in our analyses (Britton et al., 2007). This is likely because r8s collapses short branches where accurate inference of divergence time is difficult. Also, r8s employs a semiparametric smoothing process using penalized likelihood that relaxes the assumption of constant rates of evolution, where rapid rate changes on a tree are penalized (Sanderson, 2002). The comparatively sparse sampling of community trees can inflate the proportion of such rapid changes and thus result in different divergence time estimates from fully sampled phylogenies. On the other hand, PATHd8s utilizes a mean path length method, averaging the branch lengths from each node to the leaves descended from that node, which is likely less affected by taxon sampling. Furthermore, substitution rate smoothing in PATHd8 is performed locally and is thus less affected by the overall distribution of branch lengths across the entire phylogeny.

These results do not suggest that one dating method is better than another; indeed, our analyses do not allow us to compare the absolute accuracy or performance of these algorithms. Rather, our results demonstrate the different levels of sensitivity to undersampling exhibited by each dating method. For example, PATHd8s may give more consistent divergence time estimates regardless of taxon sampling than r8s, but it does not mean these estimates are more accurate (closer to true divergence times). Indeed, r8s has been shown to produce more accurate divergence time estimates than PATHd8 on average (Britton et al., 2007).

The composition of different types of errors varied greatly with metric, but was similar across simulated and empirical data. Of particular concern is the overwhelmingly high proportion of sign errors (type S) in comparisons of PD, which can lead to severe consequences when coupled with the higher error rates of community phylogenies in general (Fig. S1). For instance, in cases where PD could be used to prioritize areas and communities for conservation as frequently suggested by ecologists and conservation biologists (Faith, 1992; Pollock et al., 2015; Winter, Devictor, & Schweiger, 2013), sign errors can result in the unintended protection of less phylogenetically diverse habitats, reducing conservation efficiency. While phylogenetic diversity information may not have been frequently utilized in the past, it is increasingly becoming integrated into conservation planning and natural resource management (Laity et al., 2015).

4.3 | Error rates differ among diversity metrics and community types

In general, comparisons of alpha diversity calculated on community trees were more likely to be inaccurate than those of beta diversity. This again implies that the estimation of shorter branch lengths is more likely to be erroneous in community trees, as beta diversity comparisons involve a higher proportion of deeper nodes on average. However, despite MNND being more frequently underestimated than MPD or PD in community trees, the comparisons of alpha and beta MNND were the least likely to be erroneous across all dating methods and community types. Comparisons of MPD and PD may tend to be more erroneous because unlike MNND, which is only

concerned with the distance to the closest relative, the calculation of these metrics incorporates all the (inaccurately dated) branches in each community. In particular, the effect of inaccurate branch lengths is compounded with the calculation of MPD, as it involves the same branch multiple times, depending on the number of subtending nodes.

The discrepancies between the inferred community trees and the true community phylogeny in alpha diversity comparisons were most common when environmental filtering was present in all communities (i.e., type A). As communities structured by environmental filtering tend to be phylogenetically clustered, the calculation of diversity metrics is more likely to involve shallower nodes, which we have shown are in turn more likely to be subject to the effects of undersampling, than when communities are overdispersed. Indeed, error rates for both alpha and beta diversity comparisons were lowest when overdispersion of communities was highest (i.e., type D). The effect of community type on the accuracy of beta diversity comparisons is more complex to interpret, as calculation of beta metrics involves not only the branches within each community, but the branches that connect them as well.

Hence, we examined how the accuracy of diversity comparisons is impacted by the phylogenetic diversity of the entire species pool (Figures 5; S2). Accuracy increased with increasing PD of species pool for all trees, regardless of sampling, metric and/or community type. This is likely to be because on average, as species pool PD increases, phylogenetic distances between and within communities also increase, thus decreasing the effect of highly inaccurate shallow node dates and separating communities across greater evolutionary distances. Indeed, diversity comparisons that are more likely to involve shallow nodes and shorter branches were more sensitive to increases in species pool PD, as is demonstrated by the greater sensitivity of comparisons of alpha diversity, and MNND in particular.

We observe an exception to this pattern when all communities are overdispersed (type D). Here, the probability of erroneous MPD comparisons in community trees displays greater sensitivity to increases in species pool PD than other cases. None of the communities in type D can be drawn from exclusively monophyletic clades (Figure 2). Therefore, as species pool PD increases, both the average distance among taxa in each community (alpha MPD) and the average distance between taxa in different communities (beta MPD) must increase simultaneously. This rapidly increases the proportion of deeper, more accurately dated nodes in MPD calculations and thus decreasing the probability of making erroneous comparisons. This does not apply to measures of MNND, as they are only concerned with sister relationships. On the other hand, when some or all communities are constrained to exclusive clades (types A, B and C), increases in species pool PD can be achieved by either increases in alpha MPD or beta MPD, at least initially. For instance, when all communities are drawn from exclusive clades (type A), species pool PD can be increased to a degree by either selecting communities from clades farther apart on the phylogeny or by increasing the width of each clade from which community members are selected. In such scenarios, alpha MPD comparisons are less sensitive to increases in species pool PD, because the effects alternate between increasing community alpha MPD and beta MPD. Thus, we observe a more gradual curve of alpha MPD error probability in response to changes in species pool PD.

Despite our demonstration of the significantly elevated rates of bias and error that can result from the use of inferred community trees, with the exception of certain combinations of calibration methods and community types, the absolute error rates may appear to be within tolerable limits. However, our results are derived from highly idealized situations and represent the bare minimum levels of error possible. For instance, our alignments minimized missing data, the number of nodes between calibration points and tips were held constant, and tree topologies were fully resolved and held fixed. In practice, differences in taxon sampling will result in different alignments and different tree topologies and resolutions, which have the potential to affect the calculation and comparison of diversity metrics to an even greater degree, as the number of substitutions separating taxa and sister relationships can change drastically. While we did not test Bayesian divergence time estimation methods in this study due to computational constraints, it is likely that they would be subject to similar, if not higher levels of error when applied to community phylogenies, as prior estimations can significantly differ depending on the composition of ingroup taxa. We confirm that using inferred community phylogenies (or inferring divergence time estimates on pruned trees) leads to underestimation of phylogenetic diversity in general. Furthermore, this underestimation of divergence times does not occur evenly across the phylogeny and varies with the structure and sampling within subclades. Thus, we demonstrate that the effects of undersampling may be more severe when comparing alpha diversity between communities in general. These effects can be further compounded using metrics that consider multiple nodes and branches (e.g., MPD) over those that examine fewer (e.g., MNND). However, in real-world situations, it may be difficult to achieve good resolution at the tips of the phylogeny, and thus, calculations and comparisons of MNND could be more inaccurate. Also, it is possible that different patterns of errors and biases may emerge when considering communities that are beyond the scope of our simulations in terms of size and/or divergence.

It is generally accepted that the inclusion of additional terminal taxa has a positive impact on phylogenetic reconstruction, and our study highlights the necessity of extended taxon sampling in ecological studies with both simulated and empirical data. While the phylogenetic relationships among many species within higher taxonomic groups remain largely unresolved (Hodkinson & Parnell, 2006), we have a good understanding of the deeper evolutionary relationships of many ecologically important clades, such as birds, mammals and flowering plants, and most of these data are publically available. Increasingly, popular maximum-likelihood approaches for tree building can efficiently generate phylogenies of large numbers of taxa (Stamatakis, 2014). For those using Phylomatic (Webb and Donoghue, 2005) to infer community phylogenies, generating a better-sampled phylogeny of a monophyletic group that comprises all taxa of interest does not require any additional effort beyond identifying

a common ancestral node. While Bayesian and penalized likelihood divergence time estimation methods can be subject to computational limitations when applied to larger trees, other methods, such as BLADJ and PATHd8, are more or less instantaneous even across trees with thousands of leaves (Britton et al., 2007). Our results demonstrate the importance of calibrating trees before they are pruned to the taxa of interest, as the accurate inference of branch lengths is facilitated by the presence of additional nodes and tips. This applies to supertree approaches as well, as assembling topologies from disparate phylogenies inferred with different sources of data and methods requires recalibration of branch lengths. The observed patterns and rates of error in the inferred phylogenies were not due to the particular nature of the simulated sets of nucleotide sequences and/or the tree building approaches employed (see Appendix S1). Our results were also robust to the removal of the genus *Cuscuta*, which contained small amounts of missing data (see Appendix S2).

In conclusion, we show that an ecological sampling of taxa is not necessarily ideal for evolutionary inferences and strongly suggest that ecological studies utilizing phylogenetic frameworks make an effort to include taxa not necessarily of interest as placeholders to generate the best phylogeny possible. Along these lines, it would be instructive for researchers to re-analyse their community phylogeny data to confirm their findings and examine the extent to which taxon undersampling can have on real case studies.

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DATA ACCESSIBILITY

GenBank accession numbers of taxa used in phylogenetic analyses are provided as supplementary material. Scripts used in analyses are available at the Zenodo repository (https://doi.org/10.5281/zenodo.1173341).

AUTHOR CONTRIBUTIONS

D.S.P. and Z.X. designed the study, Z.X. performed all data collection and simulations. D.S.P. and S.W. analysed the data. D.S.P. wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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