Comparing Measures of Community Lineage Diversity across North American Forests

Kyle G. Dexter [1,2]*, **Ricardo A. Segovia** [1,3] and **Andy Griffiths** [1]

[1]   School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, United Kingdom
[2]   Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, United Kingdom
[3]   Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile
*   Correspondence: kyle.dexter@ed.ac.uk ; Tel.: +44 (0) 131 650 7439

Abstract: Lineage diversity can refer to the number of genetic lineages within species or to the number of deeper evolutionary lineages, such as genera or families, within a community. Community lineage diversity (CLD) is of interest to ecologists, evolutionary biologists, biogeographers, and those setting conservation priorities. Despite its relevance, it is not clear how to best quantify CLD. With North American tree communities as an example, we test which taxonomic and phylogenetic metrics best measure CLD. We find that phylogenetic metrics outperform taxonomic metrics. Faith's phylogenetic diversity performs well, but is skewed towards the number of lineages in recent time. The best metric is newly derived here, and termed time integrated lineage diversity (TILD). Mapping the lineage diversity of tree communities across the contiguous United States, we find a spatial pattern differing from that of species richness in key areas. The Pacific Northwest, Great Lakes Region, state of Maine, and south-eastern piedmont and coastal plain forests all emerge as areas high in lineage diversity, but relatively lower in species richness. We urge the consideration of lineage diversity, as well as species richness, when setting conservation priorities.

Keywords: Temperate forests; Species Richness; Lineage Diversity; Phylogenetic Diversity; United States; Trees; TILD

1. Introduction

The evolutionary lineage is a fundamental concept in biology, denoting a group of organisms connected by ancestor-descendent relationships [1]. Evolutionary lineages are hierarchically structured; multiple younger evolutionary lineages can be nested within an overarching older lineage, or clade. Thus, multiple genetically diverged lineages can exist within a single taxonomic species, and multiple species can belong to older evolutionary lineages, such as genera, families or orders. Knowing the number of lineages in different ecological communities and biogeographic regions gives insights into evolutionary process, biogeographic history, and conservation priorities. For example, a community or region that houses many lineages, and therefore more evolutionary history, may be a greater priority for conservation than one that houses few. However, the conservation value of lineage diversity has yet to be fully, and persuasively communicated [2–4]. Providing clear and accurate quantification of lineage diversity may assist its integration into conservation practice.

In its most basic form, counting the number of lineages in communities could consist of counting the number of species. However, the term lineage diversity is generally applied when the units are not species, but a shallower or deeper evolutionary level, i.e. within or above the species taxonomic rank. The majority of times the term lineage diversity has been used in the literature, it refers to the number of diverged genetic lineages within species (e.g., [5–9]), but it has also been used for deeper evolutionary levels (e.g., [10–14]). In this paper we focus on the latter, employing tree communities in

the contiguous United States to test various metrics by which community lineage diversity (hereafter, CLD) might be quantified using taxonomic and phylogenetic data.

Taxonomy is a hierarchical system for organising biological diversity. As such, it provides an apparently straightforward means of quantifying CLD at different evolutionary depths, for example by tallying the number of genera, families or orders in communities. However, Linnean taxonomic ranks are not 'natural' in the sense that they do not directly correlate to any precise evolutionary age. Some clades of a given taxonomic rank may actually be younger than clades of a putatively lower taxonomic rank. For example, the genus *Pinus* (Pinaceae) may be as old as 100 million years [15], which is older than most angiosperm families [16]. If one were to compare a community of four *Pinus* species with a community of four angiosperm species belonging to different genera in the same family, and CLD were estimated as the number of genera in each community, the angiosperm community would appear to have 4x higher CLD. However, all four species in the community of *Pinus* may have diverged from each other prior to the origin of the most recent common ancestor of the four species in the angiosperm community (similar to mock communities B and C in Fig. 1), which could mean that the community of *Pinus* has greater conservation value in terms of encompassing greater total evolutionary history.
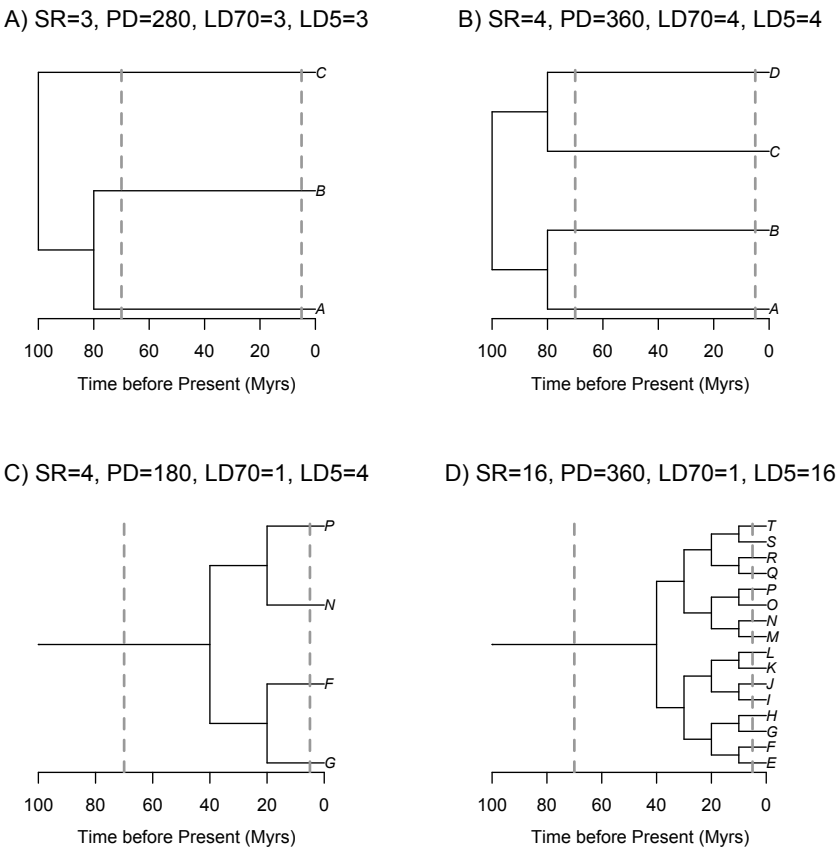
Figure 1. Example phylogenies for four communities (A,B,C,D) with contrasting species richness (SR), phylogenetic diversity (PD) and phylogenetic community structure (LD70 = number of lineages 70 Ma; LD5 = number of lineages 5 Ma). Time units are arbitrary.

The advent of molecular phylogenetics has allowed researchers to move past taxonomic approaches to quantifying CLD. Using a temporally calibrated phylogeny, one can choose a certain lineage age - X millions of years (Myrs) - and then readily estimate the number of lineages at X million years ago (Ma) in a community. Further, one could examine how the number of lineages varies at different time slices across a set of communities or geographic space (sensu Jønsson *et al.* 2011). This is

54 directly analogous to constructing a lineage through time plot for a given evolutionary clade [17], and
55 indeed, studies have proposed constructing lineage through time plots for individual communities
56 [18]. However, it is not clear at which evolutionary age, or phylogenetic depth, one should be counting
57 lineages. A community that has more lineages at one, deeper time slice might have fewer lineages at
58 another, more recent time slice (compare communities B vs. D in Fig. 1), which could be driven by
59 variation in diversification histories, community assembly, or numerous other processes. It would be
60 ideal to have a single, synthetic metric for CLD that integrates over the evolutionary history of the
61 clade being studied.

62   Faith (1992) developed a simple metric, phylogenetic diversity (PD), to quantify the evolutionary
63 history present in communities, which is calculated by summing the length of all branches in a
64 phylogeny that includes all taxa present in a community, and only those taxa. While this metric is
65 related to the number and age of evolutionary lineages present in a community, and thus may serve
66 as a proxy for CLD, Figure 1 demonstrates that inferences of CLD based on calculating PD may not
67 always be straightforward. In this contrived scenario, it seems clear that Community A has less CLD
68 than Community B and that Community C has less CLD than Community D. The calculations of PD,
69 and even species richness, would support this visual observation. Further, it seems plausible that
70 Community A has more lineage diversity than Community C, even though Community C has more
71 species. However, do Communities B and D really have identical CLD even though they have such
72 a discrepancy in species richness? Comparing Communities B and D is challenging because they
73 have such different phylogenetic structures. Community B has 4x as many lineages at 70 Ma, while
74 Community D has 4x as many lineages at 5 Ma. For this reason, researchers have suggested that the
75 amount of PD a community contains above or below that expected given its SR is a better measure of
76 CLD [12,13]. However, if we were to follow that approach, then Community C might be considered to
77 have more CLD than Community D (its ratio of PD:SR is twice that of Community D), even though
78 at all phylogenetic depths Community D has the same or more lineages than Community C. Clearly,
79 more work is needed to determine which metrics derived from phylogenies may provide the best
80 measures of CLD that integrate over evolutionary timescales.

81   The overarching goal of the present manuscript is to empirically compare different community
82 lineage diversity metrics, in order to determine the best synthetic measure of CLD over evolutionary
83 timescales. As our empirical example, we focus on tree communities in the contiguous United
84 States. These communities provide an ideal system for such an empirical study, as over 150,000 forest
85 inventory plots have been sampled in a standardised way by the U.S. National Forest Service and
86 existing time-calibrated phylogenies encompass nearly all species present in the plots. We use this
87 unparalleled community phylogenetic dataset to 1) test the ability of taxonomic and phylogenetic
88 metrics to measure CLD over multiple evolutionary ages, or phylogenetic depths and 2) map spatial
89 patterns of tree alpha CLD in the forests of the contiguous United States, which can serve as a means
90 to highlight areas of high lineage diversity for conservation attention.

2. Materials and Methods

2.1. Data Sources

93   We accessed compositional data from 177,549 plots sampled across the contiguous United States
94 by the Forest Inventory and Analysis (FIA) Program of the U.S. Forest Service [20], via the BIEN
95 package [21] for the R Statistical Environment (R Development Core Team 2018). The FIA protocol
96 records trees $\geq$ 12.7 cm diameter at breast (dbh) in four 168.3 m^2 subplots that are 36.6 m apart. The
97 main evident spatial data gaps in this dataset are the state of Louisiana and the eastern part of the state
98 of Kentucky.

99   In order to obtain a phylogeny that covered all species in the FIA tree plot inventory dataset,
100 we combined the temporally calibrated ultrametric phylogenies for North American gymnosperm
101 and angiosperm trees from Ma textitet al. 2016. We set the age of the split between angiosperms and

102 gymnosperms at 350 Ma [22]. After resolving synonyms according to The Plant List Version 1.1 (
103 http://www.theplantlist.org/), we manually added the tree species present in the FIA dataset, but
104 absent in the phylogeny. Their exact placement was based on consultations of the systematics literature
105 (see Table S1 for species added and associated literature reference), with the added taxon being placed
106 halfway along the branch leading to its sister species or clade in the phylogeny. The branch length
107 leading to the added taxon was set to a value such that the tree remained ultrametric.
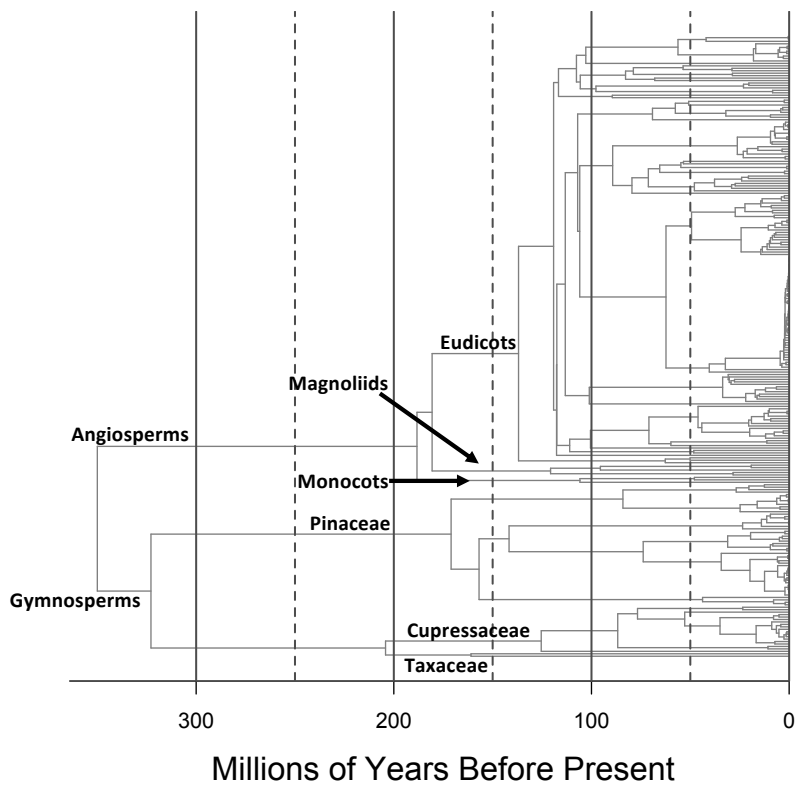
Figure 2. Phylogeny of all tree species present in the contiguous United States in the US FIA dataset, based on the phylogenies for gymnosperms and angiosperms in Ma *et al.* (2016).

108 *2.2. Lineage Diversity Metrics*

109 2.2.1. Taxonomic Measures

110   In the absence of phylogenetic data, the number of supraspecific lineages in communities can
111 be calculated as the number of taxa of a higher taxonomic rank. Classification systems are consistent
112 across angiosperms and gymnosperms up to the order level, and we therefore tabulated the following
113 taxonomic measures of lineage diversity for communities: **number of genera, number of families**
114 **and number of orders**.

115 2.2.2. Phylogenetic Measures

116   Since the advent of molecular phylogenetics, diverse metrics have been developed and
117 implemented to quantify the lineage, or evolutionary, diversity of communities from phylogenies
118 (e.g., [23–25]). We focus here on metrics that aim to quantify the 'richness dimension of phylogenetic

diversity' [26], as our interest is in 'how much' lineage diversity is in communities, not how diverged lineages are from each other in communities (e.g., as quantified by mean pairwise phylogenetic distance) or how evenly lineages are represented (e.g, as quantified by phylogenetic species evenness; [27]). In addition, conservation prioritisation is generally based on which species are present, not their relative abundance (which could reflect disturbance histories or other idiosyncratic processes), and we therefore focus on presence/absence metrics. This also increases the general utility of our results, as abundance information is not available for many datasets.

We started by calculating the most basic metric of CLD, **phylogenetic diversity**, or **PD** [19], which is the sum of all branch lengths in each community, including the branch that goes to the root of all seed plants. We also include its estimate standardised for variation in species richness. This is accomplished by calculating the first two moments of the null expectation for PD, given the number of species in the community, and using them to calculate a standardised effect size. The moments of the null distribution can be calculated by randomly shuffling the tips of the phylogeny many times, but there is an analytical expectation for these moments, which is the approach we used [28]. We refer to this metric as the **standardised phylogenetic diversity**, or **sPD**.

We also calculated two additional proposed measures of the richness dimension of phylogenetic diversity, the **phylogenetic species richness**, or **PSR** [27] and the **sum of evolutionary distinctiveness**, or **sumED** [29]. PSR can essentially be considered a measure of species richness that takes into account the phylogenetic relatedness of taxa in a community. If the community is comprised entirely of closely related species, this will produce a lower value of PSR than if the community were derived of distantly related taxa. In practice, this measure is obtained by multiplying the mean pairwise phylogenetic distance between species in a community by its species richness (and dividing by two, so that it represents distance to tips from the most recent common ancestor for each pair of species). For sumED, we first calculated the evolutionary distinctiveness of each species in our dataset, based on the entire phylogeny representing all species, following the fair proportions approach of Isaac et al. (2007). This is essentially a measure of how phylogenetically isolated each species is, relative to the given phylogeny. We then summed these evolutionary distinctiveness values for the species in each community, following [29].

As our overarching goal in this study was to quantify CLD over the full evolutionary time of the clade of study (here, seed plants), we developed an additional metric that may better capture this, which we term **time integrated lineage diversity**, or **TILD**. If one constructs a lineage through time (LTT) plot for each community (sensu [18]), one can simply integrate the area under this curve as a measure of the total lineage diversity of the community over time. In fact, this integral is mathematically identical to the phylogenetic diversity of the community, when including the root branch. However, in considering an LTT plot built from extant species, as LTT plots for extant communities are, they necessarily monotonically increase towards the present and, under a constant diversification rate, this increase is exponential. The integral therefore is necessarily weighted towards the number of lineages in recent evolutionary time compared to the number of lineages in deeper evolutionary time. Therefore, in order to downweight the number of recent lineages when calculating TILD, we log-transformed the y-axis (i.e. the number of lineages at each point in time) prior to taking the integral.

2.3. Statistical Analyses

There is wide variation in the number of individual trees sampled per plot (66 ± 65 inds, mean $\pm$ s.d.; range 1-706 inds.), and all of the lineage diversity metrics that we calculated, except sPD, were positively correlated with the number of individuals sampled (Pearson's $r = 0.58 - 0.67$). In order to obtain comparable estimates of CLD, we rarefied communities to the same number of individuals. While rarefaction can be problematic because it excludes communities from analysis below the abundance threshold used and introduces heteroscedasticity in the diversity estimate that is related to the number of individuals sampled [31], we do not know of any estimates of CLD or phylogenetic diversity that are robust to variation in sample size (in terms of number of individuals

168 sampled). While Rao's quadratic entropy has been proposed as an estimate of phylogenetic diversity
169 that is robust to variation in sample size, it measures the divergence dimension of phylogenetic
170 diversity, not the richness dimension [26], and is therefore not of interest to us here.

171   In order to determine the number of individuals to select in rarefactions, we first selected the
172 subset of communities that have at least 100 individuals (39,708 communities). We estimated the
173 species richness of these communities when rarefacted to 100 individuals (i.e. expected number of
174 species per 100 stems). We then rarefacted these communities to smaller numbers of individuals, and
175 observed how the richness estimate for a smaller number of stems correlated with the richness estimate
176 per 100 stems. Once communities were rarefacted to less than 25 stems, the correlation (pearson's r)
177 between the two richness estimates dropped below 0.95. We therefore chose 25 individuals as the size
178 for rarefied communities. We repeated rarefactions 100 times, and calculated the average of each CLD
179 metric over these 100 rarefactions.

180   In order to assess the performance of each CLD metric over the evolutionary history of seed
181 plants, we calculated the spearman's rank correlation (rho) between a given CLD metric and the
182 number of lineages at different phylogenetic depths (in intervals of 5 Myrs between the present and
183 the root of the seed plant phylogeny at 350 Ma). We used spearman's rank correlation because these
184 relationships are not necessarily linear, and because our goal is to evaluate if communities would be
185 ranked similarly, e.g. for conservation prioritisation, if counting the number of lineages at a particular
186 time slice vs. using a given CLD metric. In order to obtain an overall measure of the performance of a
187 lineage diversity metric, we then obtained the mean of the spearman's rho values at all phylogenetic
188 depths. All analyses were carried out in the R Statistical Environment (R Development Core Team)
189 using functions in the ape [33], picante [34], vegan [35] and PhyloMeasures [28] packages. The analysis
190 script is available in Appendix A.

3. Results

192   The majority of communities sampled at least 25 individuals (124,566 of 177,549 communities
193 or 70%), and were therefore included in analyses. We estimated CLD metrics for each community,
194 including constructing lineage through time (LTT) plots for each community to calculate the time
195 integrated lineage diversity (TILD). We show a sample of those LTT plots in Figure 3. The most
196 species-poor communities show little accumulation of lineages over time (Fig. 3a), as might be
197 expected given that they only have 1-2 species (12% of communities with at least 25 individuals have
198 only 1 or 2 species). The most species-rich communities have anywhere from 9 to 17 species per 25
199 stems (although only 8 of those communities have more than 15 and are not represented in the random
200 sample in Fig. 3c). Considering these species-rich communities, we see a wide range of variation
201 in when these communities accumulated lineage diversity. Although few included more than four
202 lineages before ∼120 Ma. At 150 Ma, there were twice as many gymnosperm as angiosperm lineages
203 (six vs. three; Fig. 2). By 100 Ma, the picture had changed substantially, due almost entirely to the
204 radiation of the Eudicots (Fig. 2). This radiation is evident in the LTT plots for the most species-rich
205 communities (the big jump in number of lineages at ∼120 Ma; Fig. 3c), and to a lesser degree in the
206 LTT plots for communities of average species richness (Fig. 3b). The second-largest step-change in
207 the number of lineages present in communities occurs between 5 Ma and the present, and again the
208 step-change is more pronounced in the most species-rich communities.
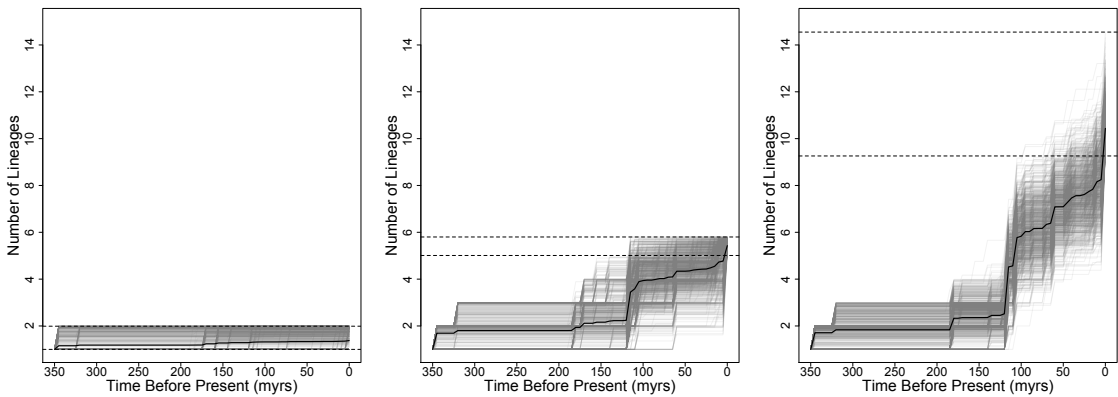
Figure 3. Lineage through time (LTT) plots for a sample of 1000 communities from a) the most species-poor communities (below 10% quantile in species richness per 25 stems), b) communities of average species richness (between the 45-55% quantiles) and c) the most species-rich communities (above the 90% quantile). The dark black lines give the mean LTT for these subsets, while the horizontal dashed grey lines show the minimum and maximum species richness per 25 stems for these subsets.

Except for standardised phylogenetic diversity (sPD), the different CLD metrics we calculated are correlated with each other (Pearson's r = 0.61-0.96) and with the number of species in communities (Pearson's r = 0.59-0.76; Fig. S1). The correlation of species richness with the number of lineages declines with increasing phylogenetic depth, dropping to very low values prior to the radiation of the Eudicots (Fig. 4). The taxonomic measures of CLD all show a similar pattern; i.e. none show a strong correlation with number of lineages prior to ~120 Ma. Because of this, none of the taxonomic measures of lineage diversity show a mean correlation over evolutionary time greater than 0.5.

The measures of lineage diversity derived from the molecular phylogeny are variable in their ability to consistently measure CLD over the full breadth of the evolutionary history of seed plants (Fig. 4). Neither sPD or sum of evolutionary distinctiveness (sumED) show high mean correlations, and these two metrics show contrasting patterns over phylogenetic depth. sPD is correlated well with the number of lineages deep in evolutionary time, while sumED shows a pattern more similar to taxonomic measures of lineage diversity. The best performing metric of lineage diversity is the newly-derived measure, time integrated lineage diversity (TILD), but phylogenetic diversity (PD) and phylogenetic species richness (PSR) also performed well. PD and PSR show stronger correlations with the number of lineages in recent evolutionary time, while TILD shows stronger correlations with the number of lineages in deeper evolutionary time.
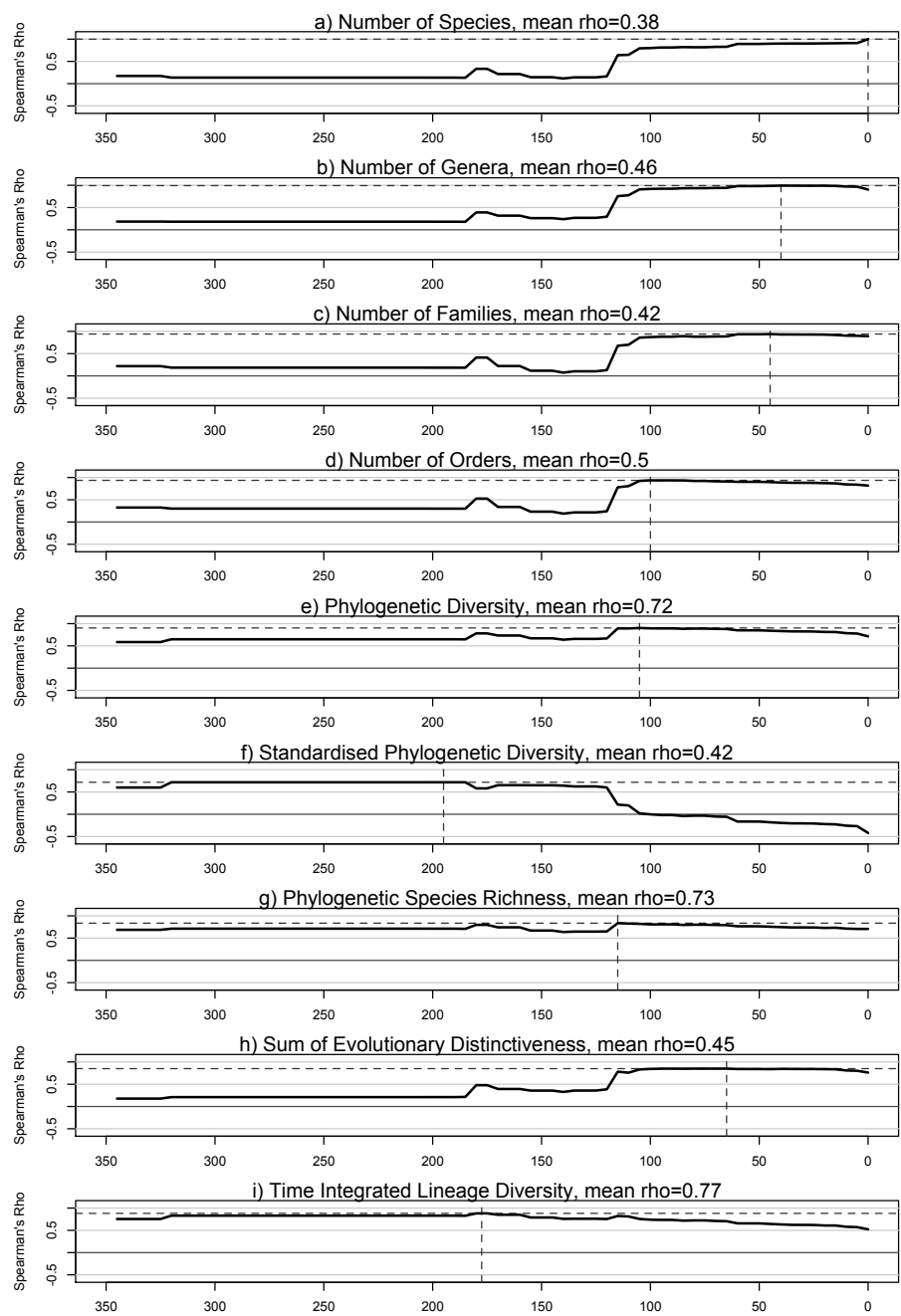
Figure 4. Spearman's rank correlations between different global measures of community lineage diversity and the number of lineages at different phylogenetic depths. The mean value of spearman's rho across all depths (excluding t = 0 and 350) is given above each plot. The phylogenetic depth at which the maximum correlation is found is marked with dashed lines going to the x and y-axes.

226   The number of species per 25 trees in plots shows clear spatial patterns across the contiguous
227   United States. Low values are generally observed west of the Mississippi River, while east of the
228   Mississippi River, low values are observed in Florida and around the Great Lakes. The highest values
229   are in the central part of the eastern United States, centred around Kentucky and Tennessee. The spatial
230   pattern of sPD contrasts strongly with that for species richness, which is not unexpected given that the
231   two measures are negatively correlated (Fig. S1). The remaining phylogenetically-derived CLD metrics
232   show spatial patterns generally similar to that for species richness, but with key areas of divergence.
233   There is more variation in CLD metrics in the western United States than there is in species richness.
234   Communities in the Great Lakes region shows higher CLD than communities immediately to their

south. The state of Maine in the far northeast of the United States also shows high lineage diversity. Meanwhile, most phylogenetic metrics of CLD show the region around the southern Appalachians to have higher CLD than regions to their north and west, whereas Fig. 5a shows them to have comparable species richness.
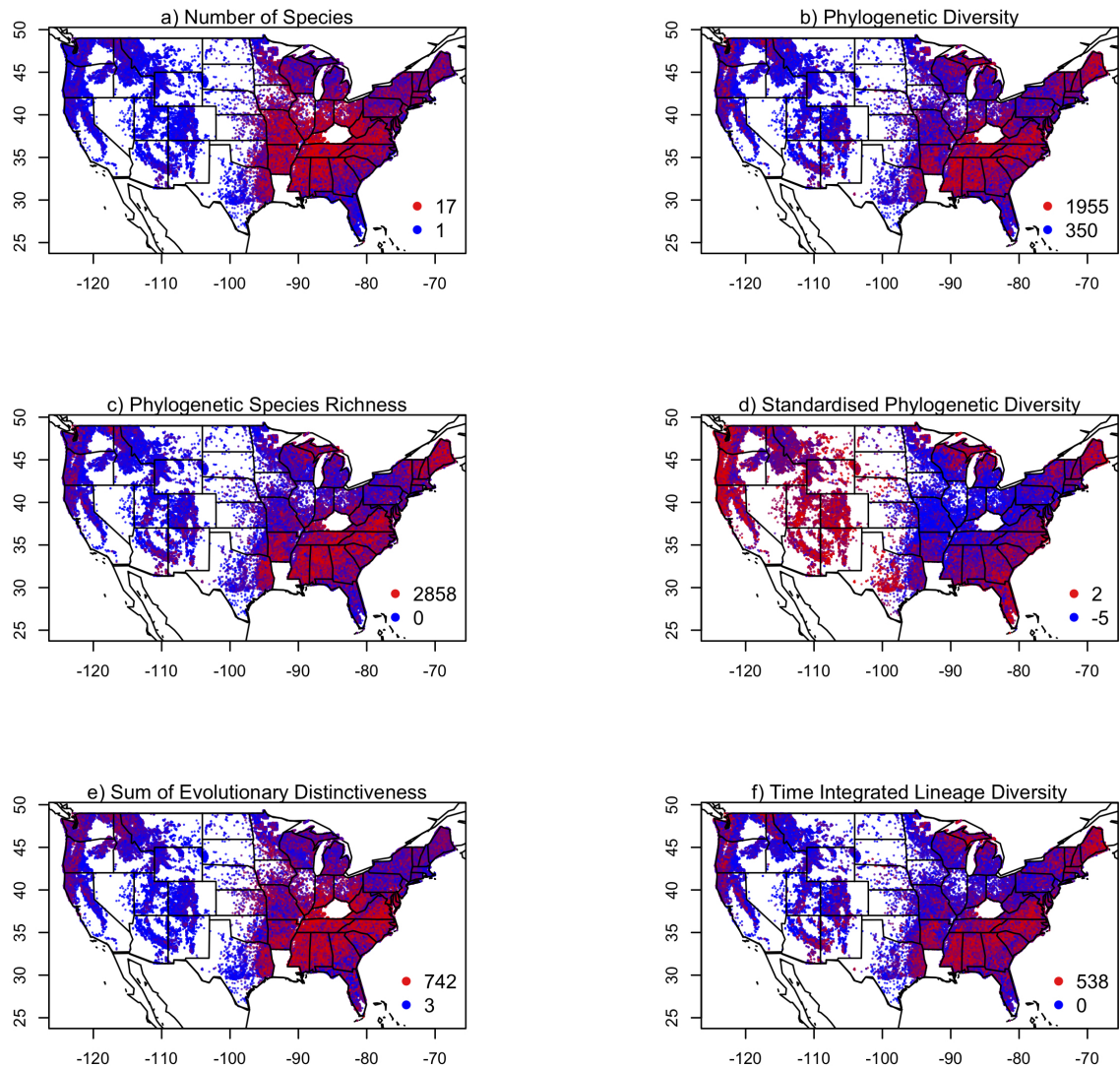
Figure 5. Spatial pattern of species richness and phylogenetically-derived community lineage diversity metrics per 25 trees for individual plots across the contiguous United States (n = 124,566 plots), with plots coloured according to their value. The legends gives the maximum and minimum values.

4. Discussion

Community lineage diversity (CLD) metrics derived from a phylogeny did a better job of capturing lineage diversity of tree communities over the full evolutionary depth of seed plants than did taxonomic metrics, such as the number of genera or families. The best performing metric was a new one, derived here, which we term time integrated lineage diversity (TILD). This metric, and all other phylogenetically-derived CLD metrics, give a different spatial pattern across the contiguous United States than that found for species richness. If prioritisation schemes were to be based solely on the number of tree species per community, the entire western half of the US would receive less conservation attention. This is because the most species-rich tree communities in the contiguous US are dominated by angiosperms, particularly Eudicots, and these are more diverse in the eastern US. Yet western US tree communities, dominated by older, relatively species-poor gymnosperm lineages, can still

250 represent substantial reservoirs of evolutionary history, as reflected in CLD values comparable to the
251 most lineage-diverse tree communities in the eastern US.

4.1. Taxonomic measures of lineage diversity

253 In many studies [12,36], species richness has been shown to be strongly correlated with
254 phylogenetic diversity (PD), and thus it has been argued that species richness may be a suitable
255 proxy for CLD [37]. Our study suggests that, at least for tree communities in the contiguous US, this is
256 not the case. Higher-level taxonomic measures that we explored, specifically the numbers of genera,
257 families and orders in communities, do not perform much better. As expected, as higher taxonomic
258 ranks are used, strong correlations with number of lineages persist deeper into evolutionary time
259 (compare the x-intercept of highest correlation for different taxonomic ranks in Fig. 3), but none of
260 the taxonomic measures provide a high correlation with number of lineages prior to ~120 Ma. This
261 is perhaps unsurprising as the majority of lineages deeper in evolutionary time are gymnosperms,
262 and all the gymnosperms in our dataset come from a single order, three families and 15 genera, while
263 angiosperms dominate the variation in these taxonomic measures of CLD with 18 orders, 35 families
264 and 68 genera. Thus, for clades with highly imbalanced phylogenies, as for seed plants, taxonomic
265 measures of lineage diversity are not likely to provide an adequate, synthetic measure of CLD [38].

4.2. Phylogenetic measures of lineage diversity

267 The best performing metric in this study, in terms of maintaining a high correlation with number
268 of lineages at all phylogenetic depths, was time integrated lineage diversity (TILD), a metric newly
269 developed here. This metric represents the area beneath a lineage through time plot where the number
270 of lineages per time slice has been log-transformed. TILD is mathematically related to PD, which
271 is identical to the area beneath a raw (i.e., non-log-transformed) lineage through time plot. PD was
272 originally conceived as a metric to aid conservation prioritisation [19], and it has always been properly
273 interpreted as a measure of the total evolutionary diversity in communities, which is certainly worth
274 quantifying. But, it is strongly skewed towards the number of lineages present in recent evolutionary
275 time, downweighting older evolutionary divergences. We suggest that researchers may use PD to
276 quantify CLD more recently in evolutionary time, and complementarily, TILD may be more suitable to
277 obtain a measure of lineage diversity for older clades. The phylogenetic species richness (PSR; [27])
278 is strongly correlated with both TILD and PD (Fig. S1) and shows a similar spatial pattern to these
279 two metrics (Fig. 5). However, as TILD and PD are both directly interpretable in terms of numbers of
280 lineages, we advocate for their use as measures of lineage diversity.

281 For this dataset, the standardised phylogenetic diversity (sPD) correlates well with the number of
282 lineages deep in evolutionary time, but not with numbers of lineages in recent evolutionary time. In
283 fact, sPD is negatively correlated with numbers of lineages less than 70 million years old. We suggest
284 that sPD may better serve as a metric of phylogenetic community structure, which is interesting in its
285 own right [39], but that it should not be used as a measure of lineage diversity in communities. Our
286 dataset appears to show a negative correlation between species richness and sPD, meaning that more
287 species-rich communities are more phylogenetically clustered. This would argue against a role for
288 competitive exclusion of closely related species in structuring tree communities in the contiguous US
289 (c.f. results of Dexter *et al.* 2017 for the Amazon). However, caution is needed in interpreting this result,
290 as sPD may artefactually decline with increasing species richness [41]. Further, more focused studies
291 of younger clades in single ecological regions have given the opposite result (e.g., [42]).

292 Like sPD, the sum of evolutionary distinctiveness in communities, sumED showed a weaker
293 mean correlation with number of lineages over the full evolutionary history of seed plants than TILD,
294 PD or PSR. In contrast to sPD, it showed weaker correlations deeper in evolutionary time and stronger
295 relationships in shallower evolutionary time (Fig. 4). In fact, sumED showed a very similar pattern to
296 taxonomic metrics of lineage diversity (Fig. 4), and of the phylogenetically-derived metrics in this study,
297 it shows the strongest correlation with taxonomic metrics (Fig. S1). As a conservation prioritisation

metric, sumED has a clear intuitive value, since it represents the totality of phylogenetic diversity in a given community that is rare in the entire dataset, but it will be sensitive to phylogenetic taxon sampling in the overall dataset, even if all taxa in a given community are present in the phylogeny (see Isaac *et al.* 2007 for full explanation of how ED is derived for each species). Conversely, PD and TILD will be insensitive to the sampling level of species not present in a given community and may therefore have more general utility.

4.3. Tree diversity patterns across the contiguous United States

In this study, we have quantified various measures of CLD at the alpha level for tree communities across the contiguous United States. Consistent with previous assessments [43,44], the most evident spatial contrast in the species richness pattern is between the eastern and western United States. To a very coarse approximation, this reflects the dominance of gymnosperms in the western United States, the dominance of angiosperms in the eastern United States, and the fact that angiosperms are a much more diverse clade than gymnosperms (even when focusing only on trees). It is notable that the differences in species richness between communities of average species richness versus the most species-rich communities arise almost entirely from diversification that happened after 120 Ma, i.e. since the radiation of the Eudicots (Fig. 3). Eudicots represent the majority of species in our dataset (Fig. 2) and the large majority of species in our most species-rich communities.

Previous studies have identified the high plateau south of the Appalachian Mountains [43], and the Florida panhandle, Alabama/Georgia border region [44], as areas of maximal tree species richness. In contrast we found the highest tree species richness in a region centred on Kentucky and Tennessee, which corresponds to the mixed mesophytic forest region [45]. The first part of the name reflects that there are no particularly dominant tree species in the region and most forest stands have a mix of dominant species. Braun (1950) recognised the exceptional tree species richness of this region and characterised it as "the association of the Deciduous Forest which occupies the area of optimum moisture and temperature conditions of North America" (p. 42). Indeed, moisture stress for plants is lower in this region of the US compared to regions southeast of the Appalachians or the entire western US, while temperatures do not reach as extreme lows as the northern parts of the contiguous US. Meanwhile, as the second part of the name, mesophytic, implies, the forests here are also found on more fertile soils compared to other forests in the US. Thus, the high alpha diversity of tree communities in this region may reflect an environment that is the most benign for the majority of tree species occurring in the contiguous United States. This is similar to the pattern found in another large biogeographic region, the Amazon, where the most species-rich tree communities are found in the western Amazon, which has more fertile soils and is subject to less moisture stress than the southern or eastern Amazon [12].

The spatial pattern of variation in tree species richness does not show a standard latitudinal gradient, which would anticipate highest species richness in the areas closest to the equator. In the western US, this may be attributable to severe moisture stress, as much of the south-western US is desert and lacks trees. Meanwhile, the south-eastern US is bordered by the Gulf of Mexico, and many species that could likely now occur in this region went extinct during Pleistocene climatic cycles [46]. Thus, biogeographic history is also playing a role in determining the composition of the species pool that is available to colonise local communities.

The spatial pattern of alpha CLD in tree communities shows several evident contrasts with the spatial pattern of species richness. With respect to tree species richness, the western US shows almost uniformly low values, at least in comparison to the eastern US, but CLD metrics show much greater variation. One evident hotspot of lineage diversity is in the temperate rain forests of the Pacific northwest, with high CLD values then extending down the western flank of the Sierra Nevada mountains. This temperate rain forest region includes the 'Miracle Mile' in the Klamath mountains of northern California which holds 18 species of conifers [47], albeit not that many occur in any single FIA plot. Lineage diversity then plummets as one crosses either the Cascade mountain range or the Sierra

Nevada mountain range. Presumably the arid conditions on the eastern side of these mountains limit tree CLD. Though species richness minima to the east of the Sierra Nevada (as well as the Rockies) have previously been noted [43], this contrast across mountain ranges is most evident when considering CLD. Other regions of notable CLD in the western US include the Chiracahua mountains of southern Arizona and northern Idaho.

In the eastern United States as well, the spatial pattern of CLD contrasts with that of species richness, although there are regions that are high for both diversity measures (e.g. the southern Appalachians). The most north-eastern state in the contiguous US (Maine) as well as the area around the Great Lakes emerge as regions of high CLD, which is presumably due to the increasing prevalence of conifers in the far north and their deep evolutionary heritage. Meanwhile, the mixed mesophytic forest region that has the highest tree species richness values does not show the highest CLD values. Higher CLD is found to the south and east of the mixed mesophytic forest region, and in the southern Appalachians and parts of the south-eastern Piedmont and coastal plain regions. The south-eastern United States was highlighted as a region of high angiosperm tree PD in a previous study based on range maps [48], and our results show this is consistent when using inventory data, and when incorporating gymnosperms into the quantification of overall seed plant CLD. The average age of angiosperm families in the southeastern US tree community is higher than anywhere else in the contiguous US [49] as this region, particularly the coastal plain, house many tree species (e.g., Sabal species [Arecaeae], textitPersea borbonia [Lauraceae], textitAnnona glabra [Annonaceae]) that belong to old, largely tropical families. This incursion of tropical lineages into the south-eastern US elevates CLD values in the south-eastern coastal plain.

5. Conclusions

Our study has shown that phylogenetically-derived metrics of community lineage diversity outperform taxonomically-derived metrics. Therefore, molecular phylogenies should play a key role in informing conservation prioritisation schemes. Thus, the continued effort to sequence all species in the tree of life receives clear support from our study. As for recommended metrics, the phylogenetic diversity of communities is a valid measure of CLD, and we do not suggest that the many previous studies to use the metric are invalid. Rather, we stress that it is biased towards the diversity of recently derived lineages, and we urge consideration of the newly developed metric TILD (time integrated lineage diversity), which may be more representative of CLD over the full evolutionary history of the clade of study.

We used an empirical dataset on tree communities of the contiguous United States to explore these different metrics of CLD. We found that the spatial patterns of CLD differ in important ways from the spatial patterns of species richness, for example by highlighting the high conservation value of temperate rainforests in the Pacific northwest. However, it would be naïve to suggest that conservationists in the United States were unaware of the high conservation value of those forests. Indeed, the tree flora of the United States is likely well enough known, such that there is already good awareness of which areas have particularly high or low conservation value with respect to tree species composition and lineage diversity. Where these metrics may be particularly useful is in less well known floras, such as in many tropical biogeographic regions. There has been one study of variation in lineage diversity across ~300 sites in the rain forests of the Amazon basin [12], but we know of no such similar study across the Congo Basin or southeast Asian rain forests, much less the more extensive tropical dry biomes.

Author Contributions: K.G.D. and R.A.S. conceived the manuscript and led analyses. A.G. contributed to analyses. All authors contributed to writing.

Funding: Please add: "This research received no external funding" or "This research was funded by NAME OF FUNDER grant number XXX." and and "The APC was funded by XXX". Check carefully that the details given are accurate and use the standard spelling of funding agency names at https://search.crossref.org/funding, any errors may affect your future funding.

Acknowledgments: R.A.S. is supported by Newton International Fellowship from The Royal Society and by Conicyt PFCHA/Postdoctorado Becas Chile/2017 N° 3140189. K.G.D. was supported by a Leverhulme International Academic Fellowship.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A.

R Codes to execute analyses.

References

1. de Queiroz, K. The general lineage concept of species, species criteria, and the process of speciation. In *Endless Forms: Species and Speciation*; D.J. Howard, S.B.E., Ed.; Oxford University Press: New York, 1998; pp. 57–75.

2. Winter, M.; Devictor, V.; Schweiger, O. Phylogenetic diversity and nature conservation: where are we? *Trends in Ecology & Evolution* **2013**, *28*, 199–204.

3. Geeta, R.; Lohmann, L.G.; Magallón, S.; Faith, D.P.; Hendry, A.; Crandall, K.; De Meester, L.; Webb, C.; Prieur-Richard, A.H.; Mimura, M.; others. Biodiversity only makes sense in the light of evolution. *Journal of biosciences* **2014**, *39*, 333–337.

4. Forest, F.; Crandall, K.A.; Chase, M.W.; Faith, D.P. Phylogeny, extinction and conservation: embracing uncertainties in a time of urgency. *Philosophical transactions Royal Society B* **2015**, *370*, 20140002. doi:http://dx.doi.org/10.1098/rstb.2014.0002.

5. Kozak, K.H.; Blaine, R.A.; Larson, A. Gene lineages and eastern North American palaeodrainage basins: phylogeography and speciation in salamanders of the Eurycea bislineata species complex. *Molecular Ecology* **2006**, *15*, 191–207.

6. Oliver, P.; Keogh, J.S.; Moritz, C. New approaches to cataloguing and understanding evolutionary diversity: a perspective from Australian herpetology. *Australian Journal of Zoology* **2015**, *62*, 417–430.

7. Milián-García, Y.; Jensen, E.L.; Madsen, J.; Álvarez Alonso, S.; Serrano Rodríguez, A.; Espinosa López, G.; Russello, M.A. Founded: Genetic Reconstruction of Lineage Diversity and Kinship Informs Ex situ Conservation of Cuban Amazon Parrots (Amazona leucocephala). *Journal of Heredity* **2015**, *106*, 573–579.

8. Becking, L.E.; de Leeuw, C.A.; Knegt, B.; Maas, D.L.; De Voogd, N.J.; Suyatna, I.; Peijnenburg, K.T.; others. Highly divergent mussel lineages in isolated Indonesian marine lakes. *PeerJ* **2016**, *4*, e2496.

9. Moritz, C.C.; Pratt, R.C.; Bank, S.; Bourke, G.; Bragg, J.G.; Doughty, P.; Keogh, J.S.; Laver, R.J.; Potter, S.; Teasdale, L.C.; others. Cryptic lineage diversity, body size divergence, and sympatry in a species complex of Australian lizards (Gehyra). *Evolution* **2018**, *72*, 54–66.

10. Linder, H.P.; Eldenas, P.; Briggs, B.G. Contrasting patterns of radiation in African and Australian Restionaceae. *Evolution* **2003**, *57*, 2688–2702.

11. Jønsson, K.A.; Fabre, P.H.; Ricklefs, R.E.; Fjeldså, J. Major global radiation of corvoid birds originated in the proto-Papuan archipelago. *Proceedings of the National Academy of Sciences* **2011**, p. 201018956.

12. Honorio Coronado, E.N.; Dexter, K.G.; Pennington, R.T.; Chave, J.; Lewis, S.L.; Alexiades, M.N.; Alvarez, E.; Alves de Oliveira, A.; Amaral, I.L.; Araujo-Murakami, A.; others. Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions* **2015**, *21*, 1295–1307.

13. Rezende, V.L.; Dexter, K.G.; Pennington, R.T.; Oliveira-Filho, A.T. Geographical variation in the evolutionary diversity of tree communities across southern South America. *Journal of biogeography* **2017**, *44*, 2365–2375.

14. Law, C.J.; Slater, G.J.; Mehta, R.S. Lineage diversity and size disparity in Musteloidea: testing patterns of adaptive radiation using molecular and fossil-based methods. *Systematic biology* **2017**, *67*, 127–144.

15. Leslie, A.B.; Beaulieu, J.; Holman, G.; Campbell, C.S.; Mei, W.; Raubeson, L.R.; Mathews, S. An overview of extant conifer evolution from the perspective of the fossil record. *American journal of botany* **2018**, *105*, 1531–1544.

16. Magallón, S.; Gómez-Acevedo, S.; Sánchez-Reyes, L.L.; Hernández-Hernández, T. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* **2015**, *207*, 437–453.

17. Raup, D.M.; Gould, S.J.; Schopf, T.J.; Simberloff, D.S. Stochastic models of phylogeny and the evolution of diversity. *The Journal of Geology* **1973**, *81*, 525–542.

18. Yguel, B.; Jactel, H.; Pearse, I.S.; Moen, D.; Winter, M.; Hortal, J.; Helmus, M.R.; Kühn, I.; Pavoine, S.; Purschke, O.; others. The evolutionary legacy of diversification predicts ecosystem function. *The American Naturalist* **2016**, *188*, 398–410.

19. Faith, D.P. Conservation evaluation and phylogenetic diversity. *Biological conservation* **1992**, *61*, 1–10.

20. Burrill, Elizabeth A.; Wilson, A.M.T.J.A.P.S.A.M.J.C.G.C.B.L.D.W. *The Forest Inventory and Analysis Database: database description and user guide version 8.0 for Phase 2. U.S.* Department of Agriculture, Forest Service, Available at web address:http://www.fia.fs.fed.us/library/database-documentation/, 2018.

21. Maitner, B.S.; Boyle, B.; Casler, N.; Condit, R.; Donoghue, J.; Durán, S.M.; Guaderrama, D.; Hinchliff, C.E.; Jørgensen, P.M.; Kraft, N.J.; others. The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution* **2018**, *9*, 373–379.

22. Harris, L.W.; Davies, T.J. A Complete Fossil-Calibrated Phylogeny of Seed Plant Families as a Tool for Comparative Analyses: Testing the 'Time for Speciation'Hypothesis. *PloS one* **2016**, *11*, e0162907.

23. Nunn, C.L.; Altizer, S.; Sechrest, W.; Jones, K.E.; Barton, R.A.; Gittleman, J.L. Parasites and the evolutionary diversification of primate clades. *the american naturalist* **2004**, *164*, S90–S103.

24. Mazel, F.; Guilhaumon, F.; Mouquet, N.; Devictor, V.; Gravel, D.; Renaud, J.; Cianciaruso, M.V.; Loyola, R.; Diniz-Filho, J.A.F.; Mouillot, D.; others. Multifaceted diversity–area relationships reveal global hotspots of mammalian species, trait and lineage diversity. *Global ecology and biogeography* **2014**, *23*, 836–847.

25. Blaimer, B.B.; Brady, S.G.; Schultz, T.R.; Fisher, B.L. Functional and phylogenetic approaches reveal the evolution of diversity in a hyper diverse biota. *Ecography* **2015**, *38*, 901–912.

26. Tucker, C.M.; Cadotte, M.W.; Carvalho, S.B.; Davies, T.J.; Ferrier, S.; Fritz, S.A.; Grenyer, R.; Helmus, M.R.; Jin, L.S.; Mooers, A.O.; others. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* **2017**, *92*, 698–715.

27. Helmus, M.R.; Bland, T.J.; Williams, C.K.; Ives, A.R. Phylogenetic measures of biodiversity. *The American Naturalist* **2007**, *169*, E68–E83.

28. Tsirogiannis, C.; Sandel, B. PhyloMeasures: A package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography* **2016**, *39*, 709–714.

29. Safi, K.; Armour-Marshall, K.; Baillie, J.E.; Isaac, N.J. Global patterns of evolutionary distinct and globally endangered amphibians and mammals. *PloS one* **2013**, *8*, e63582.

30. Isaac, N.J.; Turvey, S.T.; Collen, B.; Waterman, C.; Baillie, J.E. Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PloS one* **2007**, *2*, e296.

31. McMurdie, P.J.; Holmes, S. Waste Not, Want Not: Why Rarefying Microbiome Data Is Inadmissible. *PLOS Computational Biology* **2014**, *10*, 1–12. doi:10.1371/journal.pcbi.1003531.

32. R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2018.

33. Paradis, E.; Claude, J.; Strimmer, K. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **2004**, *20*, 289–290.

34. Kembel, S.W.; Cowan, P.D.; Helmus, M.R.; Cornwell, W.K.; Morlon, H.; Ackerly, D.D.; Blomberg, S.P.; Webb, C.O. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **2010**, *26*, 1463–1464.

35. Oksanen, J.; Blanchet, F.G.; Kindt, R.; Legendre, P.; Minchin, P.R.; O'hara, R.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H.; others. Package 'vegan'. *Community ecology package, version* **2013**, *2*.

36. Forest, F.; Grenyer, R.; Rouget, M.; Davies, T.; Cowling, R.; Faith, D.; Balmford, A.; Manning, J.; Proches, S.; van der Bank, M. Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* **2007**, *445*, 757–760.

37. Rapacciuolo, G.; Graham, C.H.; Marin, J.; Behm, J.E.; Costa, G.C.; Hedges, S.B.; Helmus, M.R.; Radeloff, V.C.; Young, B.E.; Brooks, T.M. Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas. *Nature ecology & evolution* **2018**, p. 1.

38. Miller, J.T.; Jolley-Rogers, G.; Mishler, B.D.; Thornhill, A.H. Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution* **2018**, *56*, 663–667.

39. Webb, C. Phylogenies and community ecology. *Annu Rev Ecol Evol S* **2002**, *33*, 475–505.

40. Dexter, K.G.; Lavin, M.; Torke, B.M.; Twyford, A.D.; Kursar, T.A.; Coley, P.D.; Drake, C.; Hollands, R.; Pennington, R.T. Dispersal assembly of rain forest tree communities across the Amazon basin. *Proceedings of the National Academy of Sciences* **2017**, *114*, 2645–2650, [https://www.pnas.org/content/114/10/2645.full.pdf]. doi:10.1073/pnas.1613655114.

41. Sandel, B. Richness-dependence of phylogenetic diversity indices. *Ecography* **2018**, *41*, 837–844.

42. Cavender-Bares, J.; Ackerly, D.D.; Baum, D.A.; Bazzaz, F.A. Phylogenetic Overdispersion in Floridian Oak Communities. *The American Naturalist* **2004**, *163*, 823–843, [https://doi.org/10.1086/386375]. PMID: 15266381, doi:10.1086/386375.

43. Currie, D.J.; Paquin, V. Large-scale biogeographical patterns of species richness of trees. *Nature* **1987**, *329*, 326–327.

44. Jenkins, C.N.; Van Houtan, K.S.; Pimm, S.L.; Sexton, J.O. US protected lands mismatch biodiversity priorities. *Proceedings of the National Academy of Sciences of the United States of America* **2015**, *112*, 5081–5086.

45. Braun, E.L.; others. Deciduous forests of eastern North America. *Deciduous forests of Eastern North America.* **1950**.

46. Latham, R.E.; Ricklefs, R.E. Continental comparisons of temperate-zone tree species diversity. *Species diversity in ecological communities: historical and geographical perspectives* **1993**, pp. 294–314.

47. DeSiervo, M.H.; Jules, E.S.; Kauffmann, M.E.; Bost, D.S.; Butz, R.J. REVISTING JOHN SAWYER AND DALE THORNBURGH'S 1969 VEGETATION PLOTS IN THE RUSSIAN WILDERNESS: A LEGACY CONTINUED. *Fremontia* **2016**, p. 20.

48. Ma, Z.; Sandel, B.; Svenning, J.C. Phylogenetic assemblage structure of North American trees is more strongly shaped by glacial–interglacial climate variability in gymnosperms than in angiosperms. *Ecology and Evolution* **2016**, *6*, 3092–3106.

49. Hawkins, B.A.; Rueda, M.; Rangel, T.F.; Field, R.; Diniz-Filho, J.A.F. Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. *Journal of Biogeography* **2014**, *41*, 23–38, [https://onlinelibrary.wiley.com/doi/pdf/10.1111/jbi.12171]. doi:10.1111/jbi.12171.