

# A New Phylogenetic Diversity Measure Generalizing the Shannon Index and Its Application to Phyllostomid Bats

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**ABSTRACT:** Protecting biodiversity involves preserving the maximum number and abundance of species while giving special attention to species with unique genetic or morphological characteristics. In balancing different priorities, conservation policymakers may consider quantitative measures that compare diversity across ecological communities. To serve this purpose, a measure should increase or decrease with changes in community composition in a way that reflects what is valued, including species richness, evenness, and distinctness. However, counterintuitively, studies have shown that established indices, including those that emphasize average interspecies phylogenetic distance, may increase with the elimination of species. We introduce a new diversity index, the phylogenetic entropy, which generalizes in a natural way the Shannon index to incorporate species relatedness. Phylogenetic entropy favors communities in which highly distinct species are more abundant, but it does not advocate decreasing any species proportion below a community structure-dependent threshold. We contrast the behavior of multiple indices on a community of phyllostomid bats in the Selva Lacandona. The optimal genus distribution for phylogenetic entropy populates all genera in a linear relationship to their total phylogenetic distance to other genera. Two other indices favor eliminating 12 out of the 23 genera.

**Keywords:** diversity index, biodiversity, phylogenetic entropy, quadratic diversity, Shannon index.

## Introduction

Conserving biodiversity is a central aim of environmental policy. In order to plan conservation strategies that effectively allocate limited resources, it is important to characterize the diversity present in a given community. However, there is no universally accepted biodiversity measure. Traditional indices, such as species richness, the Shannon

index (Shannon 1948), and the Simpson index (Simpson 1949), characterize diversity based on the number of species present (species richness) and the distribution of the number of organisms per species (species evenness). However, many authors (Ehrlich 1988; May 1990; Humphries et al. 1995; Crozier 1997) have argued that different species make unequal contributions to diversity and that priority in conservation decisions should be given to species with unique genetic or morphological characteristics. Newer diversity indices have been introduced to reflect these priorities, including indices that characterize only the relatedness or distinctness of species (Vane-Wright et al. 1991; Faith 1992; Nixon and Wheeler 1992; Solow et al. 1993), as well as measures that combine abundance and relatedness data. The most established of these is quadratic diversity, introduced by Rao (1982) and independently rediscovered under the name “taxonomic diversity” by Warwick and Clarke (1995), which measures the average taxonomic or phylogenetic distance between individual organisms. Other measures combining both types of data have been considered in recent research (Izsák and Papp 2000; Webb et al. 2002; Ricotta and Avena 2003; Ricotta 2004; Ricotta and Szeidl 2006; Weikard et al. 2006; Helmus et al. 2007).

A diversity measure can be considered as a valuation of the conservation priority of each species in a community. By considering how changes in species abundance affect a diversity measure, we determine the value the measure places on community members. A diversity index may favor reductions in the relative proportion of some species, for example, when a decrease in a dominant species yields a more even distribution by increasing the proportion of rare species, or a decrease in a less distinct species increases the relative abundances of more distinct species. However, it is reasonable to expect a diversity measure to favor retaining the members of a rare species, so as not to eliminate the species entirely. As is shown by Shimatani (2001), Wei-

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**Table 1:** Diversity index formulas

Index	Symbol	Formula <sup>a</sup>	Source
Species richness	$n$	$n$	
Simpson index	$D$	$-\sum_i p_i^2$	Simpson 1949
Shannon index	$H$	$-\sum_i p_i \ln p_i$	Shannon 1948
Phylogenetic diversity	$PD$	$\sum_{\text{branches } b} \ell(b)$	Faith 1992
Quadratic diversity	$Q$	$\sum_{i \neq j} d_{ij} p_i p_j$	Rao 1982
Taxonomic entropy <sup>b</sup>	$H(P, K)$	$-\sum_i p_i \ln k_i$	Ricotta and Avena 2003
Unnamed <sup>c</sup>	$H_d$	$-\sum_i p_i \ln(1 - \sum_{j \neq i} d_{ij} p_j)$	Ricotta and Szeidl 2006

<sup>a</sup>  $n$  = number of species,  $p_i$  = proportion of individuals in species  $s_i$ , and  $d_{ij}$  = taxonomic or phylogenetic distance between species  $s_i$  and  $s_j$ ;  $d_{ij}$  can be equated with the branch length of the shortest path between the corresponding leaves of a phylogenetic tree.

<sup>b</sup>  $k_i, \dots, k_n$  are species distinctness weights, normalized so that  $\sum k_i = 1$ .

<sup>c</sup> For this measure, the distances are normalized so that  $d_{ij} \leq 1$ .

kard et al. (2006), and our work below, this is not the case for some diversity measures, specifically for  $Q$ , the quadratic diversity index, and  $H_d$ , the index of Ricotta and Szeidl (2006; see table 1). There are circumstances when these indices favor eliminating species that are similar to abundant ones.

In this article, we introduce a new diversity index, the phylogenetic entropy  $H_p$ . Phylogenetic entropy places a high value on distinctive species but has the property that when members of a species become rare in proportion to other species, it is never desirable to eliminate them.

A direct formal relationship exists between  $H_p$  and the Shannon index, which is widely used, due in part to its deep mathematical roots and connections to information theory and physics. The  $H_p$  index generalizes the Shannon index in the same way that two other established indices, quadratic diversity and phylogenetic diversity, generalize Simpson’s index and species richness, respectively (fig. 1). We prove these results and compare phylogenetic entropy to other extensions of Shannon’s index (Casquilho et al. 1997; Ricotta and Avena 2003; Ricotta and Szeidl 2006).

To understand the differences between our index and other indices combining abundance and relatedness data, we analyzed the behavior of phylogenetic entropy, quadratic diversity, and  $H_d$  on bat communities in the Selva Lacandona in Chiapas, Mexico. We found that all three indices correlate with established measures of richness and evenness and prefer distributions with greater proportions of more distinct species. However, quadratic diversity and  $H_d$  favored elimination of a less distinct genus (i.e., they increased monotonically as the abundance of this genus was reduced to 0) and were optimized by distributions containing less than half of the available genera. Such situations cannot occur for the phylogenetic entropy. The optimized distribution should be understood as the logical consequence of policy decisions using a particular diversity measure. As evidence for the mathematical naturalness of our measure, an axiomatic characterization of phyloge-

netic entropy, generalizing a similar characterization of the Shannon index, is given in the appendix in the online edition of the *American Naturalist*.

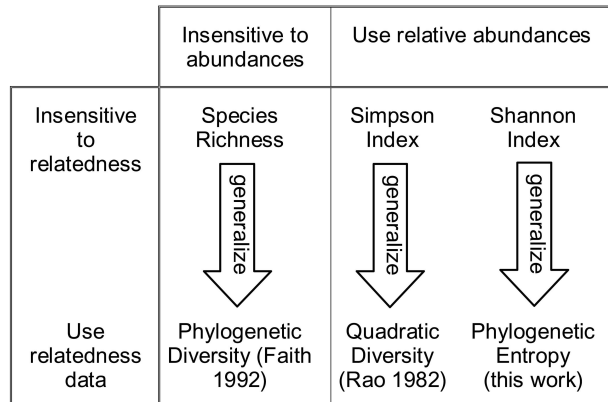
### Definition and Analysis

We define the phylogenetic entropy index of a biological community as

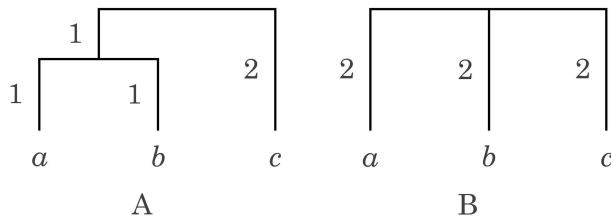
$$H_p = - \sum_{\text{branches } b \text{ of } T} \ell(b) p(b) \ln p(b), \quad (1)$$

where  $T$  is a rooted phylogenetic tree for the community,  $\ell(b)$  is the length of a branch  $b$  of  $T$ , and  $p(b)$  is the proportion of individuals in the (present-day) community who are represented by leaves descending from  $b$ . The Shannon index,

$$H = - \sum_{i=1}^n p_i \ln p_i, \quad (2)$$



**Figure 1:** Relationships between diversity measures.



**Figure 2:** Phylogenetic trees for sample ecological communities. In A, species *c* is more distinct than *a* or *b*, whereas in B, the species are equally distinct.

arises as a special case of the phylogenetic entropy if all species are equally distinct or, equivalently, if *T* has uniform branch lengths.

Our index is superficially similar to the weighted Shannon index,

$$H_w = - \sum w_i p_i \ln p_i,$$

used to measure the diversity of habitats in a landscape (Casquilho et al. 1997) and proposed as a measure of species diversity by Ricotta (2002) and Guiasu and Guiasu (2003). However, our index is evaluated in terms of the branch lengths  $\ell(b)$  and proportions  $p(b)$  reflecting the structure of the phylogenetic tree, whereas the weighted Shannon index uses a single weight for the diversity value of each species. We note that the branch proportions  $p(b)$  used in phylogenetic entropy are not mutually exclusive (multiple species may descend from a single branch) and hence do not sum to 1 as the species proportions  $p_i$  do in weighted entropy. For trees with no internal branching (e.g., fig. 2B), the two indices can be made equal by setting  $w_i$  to be the distance from the root to species  $i$ . However, in general, there is no weighting scheme that would make the two indices equivalent.

Phylogenetic entropy increases with greater distinctness of species, due to its linear dependence on the branch lengths. Given a fixed set of species, it favors distributions that are biased toward, but not dominated by, the species that are more distinct. For example, given the phylogenetic tree shown in figure 2A, in which species *c* is more distinct than species *a* and *b*,  $H_p$  attains its maximum value for the distribution  $p_a = p_b \approx 0.29, p_c \approx .41$ . In the case of figure 2B, where all species are equally distinct,  $H_p$  reduces to twice the Shannon index, and its maximum value is attained by a uniform distribution.

The relationship between phylogenetic entropy and the Shannon index parallels relationships between other diversity indices. Phylogenetic entropy and five well-known indices (defined in table 1) can be organized into three

analogously related pairs: species richness and phylogenetic diversity, Simpson index and quadratic diversity, and Shannon index and phylogenetic entropy. As indicated in figure 1, the second index of each pair generalizes the first index to incorporate relatedness data, and moreover, these generalizations are mathematically parallel in the following sense: the first index of each pair can be written in the form

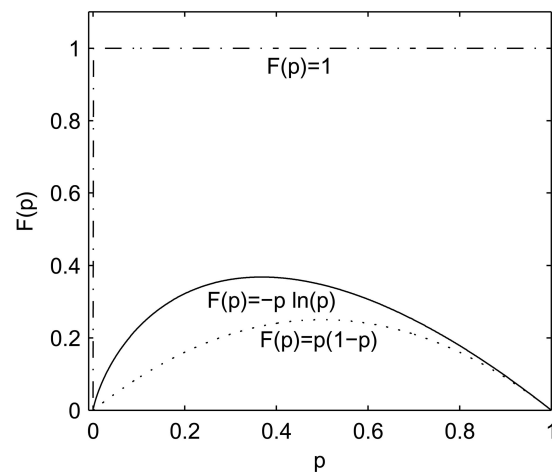
$$\sum_i F(p_i), \tag{3}$$

where  $F(p)$  is, respectively, equal to  $\chi_{(0,1)}$ ,  $p(1-p)$ , and  $-p \ln p$  for species richness, Simpson’s index, and Shannon’s index. The term  $\chi_{(0,1)}$  is an indicator function that has value 1 for all  $p > 0$  but has value 0 for  $p = 0$ , i.e., when there is no member of a species. Analogously, the second index can be written in the form

$$\sum_{\text{branches } b} \ell(b) F(p(b)), \tag{4}$$

using the corresponding  $F$  for the first index. As a consequence, the second index of each pair reduces to the first in the case where *T* has uniform branches of length 1. That these indices can be written in forms (3) and (4) is manifest except in the cases of the Simpson index, which was shown by Patil and Taillie (1982) to have form (3), and the quadratic diversity index, which is shown in the appendix.

The properties of a diversity index of the form (3) or (4) can be inferred from the shape of  $F(p)$  (fig. 3). In particular, the sensitivity of an index to the introduction



**Figure 3:** Choices for the function  $F(p)$  describing diversity measure dependence on species proportion:  $F(p) = \chi_{(0,1)}$  increases the most sharply at  $p = 0$ , followed by  $F(p) = -p \ln p$  and  $F(p) = p(1-p)$ .

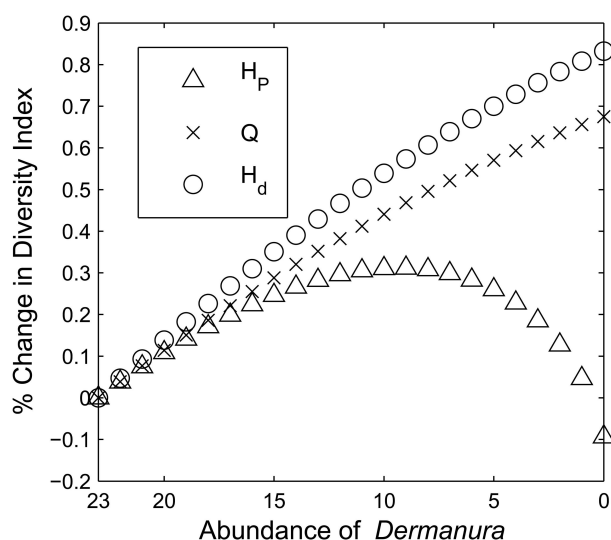


Figure 4: Change in diversity indices as the abundance of *Dermanura* in the forest habitat is reduced to 0.

or elimination of a species is dictated by the steepness by which  $F$  increases when  $p$  is increased from 0. Indices based on presence or absence of species use  $F(p) = \chi_{(0,1]}$ , which jumps discontinuously from 0 to 1 at  $p = 0$ . These indices are more sensitive than indices incorporating abundance, for which the corresponding func-

tions  $F(p)$  are continuous. Among the continuous choices for  $F(p)$ ,  $F(p) = -p \ln p$  has an unbounded derivative for small  $p$ , which leads to greater sensitivity than indices using  $F(p) = p(1 - p)$ , the derivative of which is bounded.

Indices used to support conservation policy should embody the diversity characteristics we value, including the number of species, their taxonomic or genetic distinctness, and the evenness of their distribution. In the interest of promoting evenness and distinctness, diversity indices may favor reducing the relative proportions of more abundant or less distinct species. However, indices may be expected to protect individuals of rare species. This property, termed “weak species monotonicity” by Weikard et al. (2006), ensures that the goals of promoting diversity and maintaining species richness do not conflict.

It is shown in our case study (fig. 4) and elsewhere (Shimatani 2001; Izsák and Szeidl 2002; Weikard et al. 2006) that  $Q$ ,  $H_d$ , and other indices combining abundance and relatedness data may increase monotonically as a less distinct species is reduced to 0 members, violating weak species monotonicity. We prove in the appendix that phylogenetic entropy always satisfies weak species monotonicity, due to the divergence of the derivative of  $F(p) = -p \ln p$  as  $p$  is decreased to 0.

The taxonomic entropy of Ricotta and Avena (2003) also satisfies this property. However, due to the choice of

Table 2: Phyllostomid genus abundances in Selva Lacandona habitats

Genus	Forest	Cacao	Oldfield	Cornfield
<i>Artibeus</i> (Neotropical fruit bat)	149	178	86	96
<i>Carollia</i> (short-tailed fruit bat)	121	259	342	85
<i>Centurio</i> (wrinkle-faced bat)	1	2		2
<i>Chiroderma</i> (big-eyed bat)			1	5
<i>Choropterus</i> (big-eared woolly bat)	5			
<i>Dermanura</i> (small fruit-eating bat)	23	17	17	18
<i>Desmodus</i> (vampire bat)	4	3		1
<i>Diphylla</i> (hairy-legged vampire bat)	1		1	
<i>Enchisthenes</i> (velvety fruit-eating bat)	1			
<i>Glossophaga</i> (long-tongued bat)	35	73	103	85
<i>Hylonycteris</i> (Underwood’s long-tongued bat)				2
<i>Lamproncycteris</i> (orange-throated bat)	1			
<i>Lichonycteris</i> (dark long-tongued bat)				1
<i>Micronycteris</i> (big-eared bat)		2	1	
<i>Mimon</i> (golden bat)	2	1	4	
<i>Phyllostomus</i> (spear-nosed bat)	5		5	
<i>Platyrrhinus</i> (broad-nosed bat)	6	10	17	18
<i>Sturnia</i> (yellow-shouldered bat)	56	137	102	234
<i>Tonatia</i> (round-eared bat)	1	4		1
<i>Trachops</i> (fringe-lipped bat)	2			
<i>Uroderma</i> (tent-making bat)	7	4	2	4
<i>Vamyrassa</i> (yellow-eared bat)	1	3		
<i>Vampyrodes</i> (great stripe-faced bat)	1			
Total	422	693	681	552

Source: Adapted from Medellín et al. (2000).

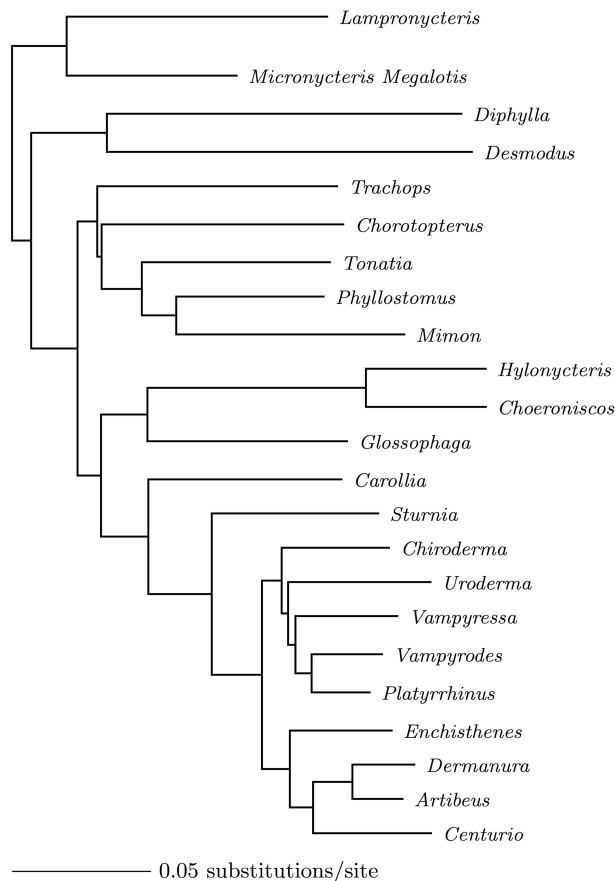


Figure 5: Molecular phylogeny of phyllostomid bat genera in Selva Lacandona habitats, adapted from Baker et al. (2003).

weights used in this index (table 1), it favors increasing the abundances of less distinct species over those of more distinct ones, counter to a conventional understanding of diversity.

### Case Study

To further compare phylogenetic entropy with other indices, we investigated the behavior of  $H_p$ ,  $Q$ , and  $H_d$  on communities of bats in the Selva Lacandona in Chiapas, Mexico. We used data provided by Medellín et al. (2000), who surveyed bat communities (primarily of the family Phyllostomidae, or leaf-nosed bats) in four habitats of the Selva Lacandona: rainforest, cacao plantations, inactive agricultural plantations with secondary vegetation, and corn plantations. (These habitats are hereafter referred to as forest, cacao, oldfield, and cornfield, respectively.) They found that the diversity of bats (measured using species richness, the Shannon index, number of rare species, and relative abundance of the most common species) decreases

with increasing levels of habitat disturbance, indicating that bat diversity may be a useful indicator of habitat integrity.

We combined this abundance data with a phylogenetic study of Phyllostomidae conducted by Baker et al. (2003). Using evidence from mitochondrial DNA and Recombination-Activating Gene-2 sequences, this study organized 48 of the 53 phyllostomid genera into a phylogenetic tree with explicit branch lengths. Though the phylogeny of Phyllostomidae is still the subject of debate (Wetterer et al. 2000; Jones et al. 2002), the analysis of Baker et al. (2003) provides an ample starting point for the study of phylogenetic diversity measures on this family.

In order to apply the phylogeny of Baker et al. (2003) to the abundance data of Medellín et al. (2000), we considered only the phyllostomid bats that were surveyed and grouped them by genus. All genera found in the four habitats are represented in the phylogenetic study except *Lichonycteris* (dark long-tongued bats), of which one individual was found. In order to include this individual in our study, we considered it to belong instead to genus *Choeronicos* (long-tailed bats), which has been shown in other studies (e.g., Carstens et al. 2002) to occupy a similar phylogenetic position relative to the other genera sampled. Because only a single individual of this genus was found, the effects of this substitution are minimal. The abundance data grouped by genus are shown in table 2, and the phylogenetic tree showing only the relevant genera is given in figure 5.

We used three numerical tests to analyze the indices. First, we evaluated their values in the four habitats and compared the results with other established indices. Second, we evaluated the change in the indices as the abundance of a close relative to a dominant genus was reduced to 0. Finally, we found the distributions that maximize the three indices, which indicate the logical consequence of policy decisions based on them. The indices are concave, so global maxima can be obtained using conventional algorithms (we used optimization commands in Maple). Since only genus-level information is available, the measures were evaluated for diversity at the genus rather than species level.

Table 3: Diversity index values for bat habitats

Index	Forest	Cacao	Oldfield	Cornfield
Genus richness	17	13	12	14
Simpson index	.7647	.7432	.6852	.7466
Shannon index	1.788	1.576	1.474	1.626
Phylogenetic diversity <sup>a</sup>	1.432	.9806	.9212	.972
Quadratic diversity <sup>a</sup>	.0614	.05951	.05658	.059
Phylogenetic entropy <sup>a</sup>	.1333	.1176	.1135	.1178
$H_d$	.4974	.4683	.4444	.4644

<sup>a</sup> Branch length units are in substitutions per site.

**Table 4:** Genus abundances in the maximizing assemblages for  $H_p$  and  $Q$ 

Genus	$H_p$ maximizer	$Q$ and $H_d$ maximizer <sup>a</sup>
<i>Artibeus</i>	.01	
<i>Carollia</i>	.035	
<i>Centurio</i>	.033	.08
<i>Chiroderma</i>	.016	
<i>Chorotopteris</i>	.054	.015
<i>Dermanura</i>	.019	.01
<i>Desmodus</i>	.118	.185
<i>Diphylla</i>	.114	.176
<i>Enchisthenes</i>	.015	
<i>Glossophaga</i>	.041	
<i>Hylonycteris</i>	.064	.106
<i>Lampronycteris</i>	.087	.124
<i>Lichonycteris</i>	.064	.106
<i>Micronycteris</i>	.041	
<i>Mimon</i>	.07	.112
<i>Phyllostomus</i>	.028	
<i>Platyrrhinus</i>	.004	
<i>Sturnia</i>	.031	
<i>Tonatia</i>	.039	
<i>Trachops</i>	.053	.005
<i>Uroderma</i>	.036	.081
<i>Vamyressa</i>	.017	
<i>Vampyrodes</i>	.01	

<sup>a</sup> The maximizing assemblages for  $Q$  and  $H_d$  agree to within  $10^{-6}$  in the genus proportions.

## Results

The diversity index values in the four habitats are given in table 3. All indices ranked the forest and oldfield habitats as the most and least diverse, respectively. Of the remaining two habitats, the cacao plantation was rated more diverse by four indices (genus richness, the Shannon index, the Simpson index, and phylogenetic entropy). The remaining three indices ranked the cornfield as more diverse.

In the forest habitat, the minor genus *Dermanura* is a close relative to the dominant genus *Artibeus* and may therefore be considered a lower conservation priority. Some diversity indices may favor reductions in *Dermanura* abundance in order to increase the relative abundances of more distinct species. We considered abundance values between 0 and 23 individuals for *Dermanura*, leaving other abundances fixed, and calculated the change in the indices (fig. 4). Both  $Q$  and  $H_d$  favor reducing the abundance to 0, whereas  $H_p$  is maximized for 9 individuals.

The genus assemblages that maximize each index are given in table 4. Interestingly, the distributions that maximize  $H_d$  and  $Q$  coincide to within  $10^{-6}$  in the genus proportions. These distributions contain 11 genera, spread more or less evenly through the phyllostomid subfamilies. The distribution that maximizes  $H_p$  contains all 23 genera

and is ranked more diverse by every diversity index aside from  $Q$  and  $H_d$  (table 5).

The abundance of a genus in the maximizing distributions correlates with its total phylogenetic distance to all other genera (fig. 6), though the relationship is stronger for phylogenetic entropy ( $R^2 = 0.946$ ) than for  $Q$  and  $H_d$  ( $R^2 = 0.703$ ).

## Discussion

Our findings suggest that the diversity indices we compared value richness, evenness, and distinctness. This can be seen from the index values in the four habitats, for which the indices correlated with genus richness, evenness indices (Shannon's index and Simpson's index), and phylogenetic diversity, a measure of distinctness. However,  $Q$  and  $H_d$  both favor complete elimination of a less distinct taxon, while  $H_p$  favors the preservation of all taxa.

The observation that the maximizing distributions for  $Q$  and  $H_d$  are similar suggests a close relationship between these indices. In the expression

$$H_d = - \sum_i p_i \ln \left( 1 - \sum_{j \neq i} d_{ij} p_j \right),$$

the distances  $d_{ij}$  are normalized by dividing by the maximum possible distance. If the distances between species are small compared with the maximum distance, the values of  $\sum_{j \neq i} d_{ij} p_j$  will be small. Using  $\ln(1 - x) \approx -x$  for small  $x$  yields

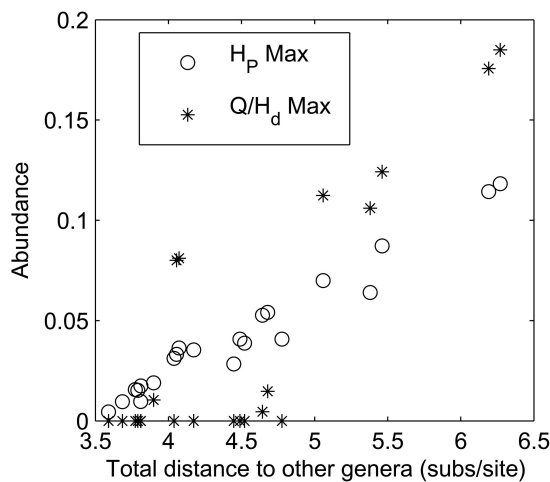
$$H_d \approx - \sum_i p_i \left( - \sum_{j \neq i} d_{ij} p_j \right) = 2Q.$$

This suggests that  $H_d$  and  $Q$  are similar for many communities.

Shimatani (2001) was the first to recognize that maximizing quadratic diversity can decrease richness. As noted by Pavoine et al. (2005), this occurs only when the leaves of the phylogenetic tree are different distances from the

**Table 5:** Diversity index values on the index-maximizing assemblages

Index	$H_p$ maximizer	$Q$ and $H_d$ maximizer
Genus richness	23	11
Simpson index	.935	.871
Shannon index	2.899	2.138
Phylogenetic diversity	1.6982	1.1253
Quadratic diversity	.1136	.1197
Phylogenetic entropy	.2963	.2628
$H_d$	1.227	1.347



**Figure 6:** Genus abundances in the maximizing genus distributions for the three indices plotted against the total phylogenetic distance from a genus to all other genera.

root. In such situations,  $Q$  and  $H_d$  can favor eliminating the species that are less distinct (relative to the other species present), thereby maximizing interspecific distances. Phylogenetic entropy does not favor eliminating species for any tree and appears to favor distributions in which the abundance of a species is linearly related to its aggregate distance to all other species.

### Conclusion

Phylogenetic entropy generalizes the Shannon index to reflect the priority of preserving highly distinct species. Unlike when using quadratic diversity and some other measures combining abundance and relatedness data, basing conservation priority on phylogenetic entropy also protects species richness. These qualities make our index attractive for diversity studies in which both abundance and phylogenetic data are relevant and available.

The general forms (3) and (4) can be used to create a variety of indices, some of which may have significant special properties in the context of biodiversity measurement. A more thorough investigation of the link between the properties of the function  $F$  and the behavior of the corresponding diversity index may yield useful indices as well as insight into mathematical properties of diversity.

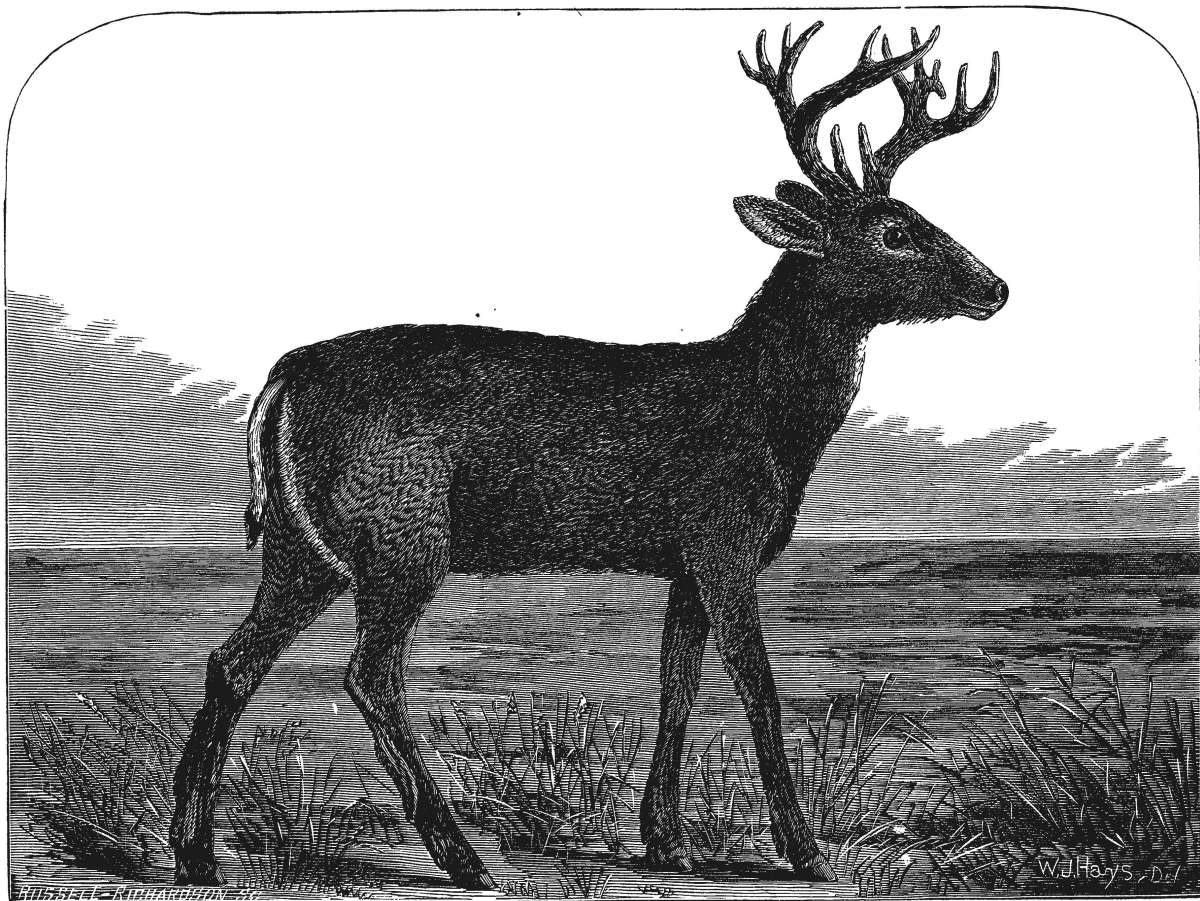
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