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A supplementary tool to existing approaches for assessing ecosystem community structure

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Abstract

Measures of biological or species diversity are central to ecology and conservation biology. Although there are several commonly used indices, each has shortcomings and all vary in the relative emphasis they place on the number of species and their relative abundance. We propose utilizing Fisher Information, not as a replacement for existing indices, but as a supplement to other indices because it is sensitive to community structure. We demonstrate how Shannon's and Simpson's diversity indices quantify the diversity of two different systems and how Fisher Information can enhance the analyses by comparing, as example, body size, and phylogenetic diversity of the different communities. Fisher Information is sensitive to the order in which species are entered into the analysis, and therefore, it can detect differences in community structure. Thus, the Fisher Information index can be useful in helping understand and analyze biodiversity of ecosystems and in comparing ecological communities.

Keywords

biological diversity; community structure; diversity indices; Fisher Information; randomization; resampling; Shannon index; Simpson index

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1 Introduction

What is biodiversity? Magurran (2004) defines biodiversity as “the variety and abundance of species in a defined unit of study.” Measures of biological or species diversity are central to ecology and conservation biology (e.g., MacArthur, 1965, Magurran, 2004, Pielou, 1975, Whittaker, 1960, Williams, 1964). If appropriate conservation policies are to be implemented, then appropriate measures of community structure must continue to be developed (Butturi-Gomes et al., 2017). Buckland et al. (2005) assert that no single index can capture all aspects related to the dynamics of biodiversity. Thus, it becomes critical to develop informative, interpretable diversity measures (Jost, 2006). Whittaker (1960, 1972) defined the concepts of species diversity within and among communities, and numerous indices have been proposed to capture this information (e.g., see Roy et al., 2004). Although there are several indices that attempt to capture or quantify diversity, each has shortcomings and all vary in the relative emphasis they place on the number of species and their relative abundance (Magurran, 2004, Sanjit and Bhatt, 2005). Numerous articles and books describe the different measures of biological diversity, as well as their strengths and weaknesses (e.g., Magurran, 2004, Roy et al., 2004). Although this is a subject of debate, no single index is best for all purposes (e.g., Wilson et al., 1996). Nonetheless, some of the most commonly employed metrics include species richness, Shannon-Wiener index (H' , commonly referred to as Shannon index), and the inverse of Simpson's concentration ($1/D$, commonly referred to as Simpson's index; Lande, 1996).

The simplest way to describe an ecological community is by using species richness: the number of species in a defined area (e.g., Gotelli and Colwell, 2001, MacArthur and Wilson, 1967, Purvis and Hector, 2001). However, the presence of a single individual of a species carries the same weight as a population that contains numerous individuals. The Shannon index attempts to account for the relative abundance, but it is weighted towards uncommon or rare species (e.g., Magurran, 1988, Peet, 1974, Sanjit and Bhatt, 2005). Simpson's index (D), on the other hand, quantifies how evenly species are distributed across a community and tends to ignore rare species (Magurran, 2004, Peet, 1974). As a diversity index, $1/D$ is weighted towards the abundant species (Magurran, 2004, Peet, 1974). Another drawback of Shannon and Simpson indices is that they may not identify differences between communities when the number of species and their relative abundances are similar.

To demonstrate these drawbacks, we present two extreme examples, which result in similar values and are indistinguishable statistically by the Shannon and Simpson indices. In the first example, two communities are compared that contain entirely different species but the relative abundances are similar. Consider the following: community 1 contains 17 individuals and three species (10 of species A, 5 of species B, 2 of species C) and community 2 has 17 individuals and three species (10 of species D, 5 of species E, 2 of species F). In the second example, two communities have the same species, but the relative abundances are inverted such that community 1 has 17 individuals from three species (10 of species A, 5 of species B, 2 of species C) and community 2 has 17 individuals from three species (2 of species A, 5 of species B, 10 of species C). In these examples, the communities are equally diverse ($H' = 0.9238$ and $1/D = 0.5882$). In such simple examples, the differences in community structure are obvious. Real community comparisons are unlikely

to be so straightforward and, as the number of species and individuals increases, differences may not be as readily apparent. Nonetheless, Shannon and Simpson's indices are some of the most commonly used measures of diversity (De 2007).

Shannon and Simpson's indices are unable to represent structural information embodied in a community or ecosystem (Brooks, 2003, Roy et al., 2004); the reason they do not identify differences in the above examples is evident in their respective mathematical formulas:

$$H' = - \sum_{i=1}^s p_i \log(p_i) \quad (1)$$

where s is the number of species and p_i is the proportion of the i^{th} species at each site and where

$$D_s = \sum_{i=1}^s \frac{n_i(n_i - 1)}{N(N - 1)} \quad (2)$$

the diversity index equals $\frac{1}{D}$, and where n_i = number of individuals of species i and $N = \sum n_i$ (Solow 1993). Because the proportions are added, the order in which species are entered is irrelevant.

To enhance information obtained from H' and $1/D$ (and other possible indices), we propose utilizing Fisher Information (FI) as supplement to other indices of community structure. Information theory has been used before in ecology and, in fact, Shannon index is based on information theory (e.g., Ulanowicz, 2001). The strength of FI is that it is highly dependent on how groups (e.g., species) are ordered, and the order of species can be varied based on the question being asked. For instance, species in a community can be ordered by rank of abundance, with species of greatest abundance listed first followed by subsequent numbers of other species. In an example of comparing communities, species also could be ordered by body mass to test community assembly rules (e.g., Allen et al., 2006, Levin et al., 2001, White et al., 2007), by trophic or functional groups to compare energy flow (e.g., Blackburn et al., 2005, Dauby et al., 2001, Downing and Leibold, 2002, Petchey et al., 2004, Tilman, 2001), or by phylogeny to compare phylogenetic diversity (e.g., Inagaki et al., 2003, Kelly et al., 2008, Martin, 2002, Nehring and Puppe, 2004). In all the above cases H' and $1/D$ would be the same for a given community irrespective of how the species are ordered. FI, on the other hand, is sensitive to community structure and its value would depend on how the species are ordered. Therefore, we suggest FI as a structure sensitive tool to augment, not replace, existing diversity indices. We will demonstrate the utility of FI by comparing it with Shannon and Simpson indices.

2 Materials and Methods

2.1 Fisher Information

Ronald Fisher developed Fisher Information as a measure of indeterminacy, and the Fisher Information concept has been used as a unifying principle of physical laws (Frieden, 2004). A specific formulation of Fisher Information has been used as a measure of order in dynamic complex systems such as ecosystems (Fath et al., 2003, Karunanithi et al., 2008). We propose using Fisher Information based on proportional observed relative abundance (p_i) as a new index of community structure. Fisher Information is formally given for discrete data by,

$$FI = \sum_{i=1}^s \frac{1}{p_i} \left[\frac{\Delta p_i}{\Delta i} \right]^2 \equiv \sum_{i=1}^s \frac{1}{p_i} [\Delta p_i]^2 \quad (3)$$

Here, $p_i = \frac{n_i}{N}$ where, n_i is the number of individuals of species i and N is the total number of individuals in the community (i.e. $N = \sum n_i$). The ratio $\frac{\Delta p_i}{\Delta i}$ represents the slope of proportions (i.e., capturing local fluctuations in species proportions) between adjacent species, and s is the number of species in the community. We have simplified Equation 3 by noting that $\Delta i = 1$ for adjacent species, and by replacing the proportion p_i with the amplitude q_i defined by $q_i^2 \equiv p_i$, to give

$$FI = 4 \sum_{i=1}^s \Delta q_i^2 \approx 4 \sum_{i=1}^s [q_i - q_{i+1}]^2 \quad (4)$$

This expression has the benefit of eliminating the division by p_i , which can be numerically problematic if p_i happens to be a small number. If you compare Equations 1, 2 and 4, you see that Equations 1 and 2 are additive indices of species proportions (and hence they are not sensitive to the order in which the species are arranged) whereas Equation 4 is an additive index of slopes of proportions between adjacent pairs of species (and, hence, it is sensitive to the order in which the species are arranged; Fig. 1). Thus, FI is a useful index when combined with Shannon and Simpson indices for comparing and analyzing community structure.

Using existing data sets, we compared two vastly different sets of small mammals: one from the grasslands of North America and one from the jungles of Borneo. We demonstrate how Shannon's and Simpson's diversity indices quantify the diversity of the two systems, and how FI can enhance the analyses by comparing body size and phylogenetic diversity of each. Our goal is not to delve into alpha, beta, or gamma diversity, but to demonstrate how FI can be used to augment some commonly used diversity indices, and reveal information on community structure.

2.2 Small Mammal Communities

Data came from two different published studies of small mammals. The first dataset (hereafter referred to as Hays) came from Hopton and Choate (2002), in which they examined the effect of an interstate highway on movement of small mammals between the triangles of median vegetation at exit/entrance ramps and the adjacent roadside vegetation in North American mixed-grass prairie. The second dataset (hereafter referred to as Borneo) came from Wells et al. (2004), in which they investigated how space is partitioned by small mammals in a Borneo forest by comparing use of terrestrial and arboreal space. Both studies provided species lists and abundance data (Hopton and Choate, 2002, Wells et al., 2004).

2.3 Data Analysis

To compare communities, we first ordered the species from the Hays dataset according to a decreasing rank abundance (i.e., the most abundant species is first, followed by the second most abundant species, then third most abundant, etc.; Table 1) and we computed an observed H' , $1/D$, and FI for each community using equations (1), (2), and (4) accordingly. The difference between the observed H' of the community in the center median and the observed H' of the community in the roadside was calculated as an absolute value of the median community minus the roadside community (e.g., $|H'_{\text{median}} - H'_{\text{roadside}}|$). The difference was computed between the median community and the roadside community for $1/D$ and FI as well. We created confidence intervals using a randomization technique that involved conducting 10,000 random samples using resampling and identifying where the calculated value falls within the randomized sample (Solow 1993). Resampling, a randomization technique (e.g., bootstrap), is more appropriate than parametric techniques because most data are not from random samples from known populations (Edgington, 1995, Lehman, 1975). In brief, resampling randomly selects points from the sample N times and calculates a P -value from the N points (see Efron and Tibshirani (1993) for a more detailed description). The relative position of the observed value to the distribution of the N sampled values produces an estimated P -value. Note that when all 10,000 of the randomized differences are greater than or less than the observed value, the estimated P -value equals 0. Next, we ordered species according to increasing body mass and by phylogeny following organization in Wilson and Reeder (2005) and repeated the analyses. The process was repeated for the Borneo dataset (Table 2), comparing terrestrial and arboreal communities with three different orderings.

All calculations were coded in *R* (version 2.7.1; CRAN 2008) to calculate H' , $1/D$, and FI (Appendix 1). To make the results of the randomization repeatable, we fixed the random seed. We verified the results of our randomization of H' and $1/D$ with a t -test for significant differences between communities (Zar 1999). Taylor (1978) suggested that if H' is calculated for several samples, the indices themselves would be normally distributed making parametric tests such as the t -test applicable.

3 Results

Hays Data.—The median and roadside communities from the Hays data set did not differ in diversity when arranged according to decreasing rank abundance as measured by H' or $1/D$

($H'_{\text{median}} = 1.0829$, $H'_{\text{roadside}} = 1.2553$, $P = 0.0698$; $1/D_{\text{median}} = 2.3763$, $1/D_{\text{roadside}} = 2.6449$, $P = 0.3004$; Table 3) or FI ($FI_{\text{median}} = 0.5915$, $FI_{\text{roadside}} = 0.6857$; $P = 0.5355$). Reordering the communities according to increasing body mass had identical results for H' and $1/D$, but FI values for the two communities were significantly different ($FI_{\text{median}} = 4.9515$, $FI_{\text{roadside}} = 3.7760$; $P = 0.0485$; Table 3). Phylogenetic ordering revealed no difference between communities as measured by H' , $1/D$, or FI ($FI_{\text{median}} = 6.2413$, $FI_{\text{roadside}} = 4.8588$; $P = 0.0541$; Table 3), although the difference between the observed FI values was marginally non-significant when arranged by phylogeny (actually, when the random seed is not fixed, sometimes $P < 0.05$).

Borneo Data.—Diversity indices of the terrestrial and arboreal communities were significantly different from each other when ordered by rank abundance ($H'_{\text{terrestrial}} = 2.4594$, $H'_{\text{arboreal}} = 1.5907$, $P = 0$; $1/D_{\text{terrestrial}} = 10.2613$, $1/D_{\text{arboreal}} = 3.1449$, $P = 0.0037$; Table 3). Observed FI values for the two communities were significantly different as well ($FI_{\text{terrestrial}} = 1.2327$, $FI_{\text{arboreal}} = 3.7135$, $P = 0.0001$; Table 3). When the Borneo data were arranged according to increasing body mass H' and $1/D$ values remained unchanged, and observed FI values were not significantly different with this ordering ($FI_{\text{terrestrial}} = 2.2296$, $FI_{\text{arboreal}} = 3.9163$; $P = 0.0921$; Table 3). Reordering the communities according to phylogeny produced identical results for H' and $1/D$, but the observed FI values indicate the two communities are phylogenetically different ($FI_{\text{terrestrial}} = 1.3482$, $FI_{\text{arboreal}} = 5.0607$; $P = 0.0001$; Table 3).

4 Discussion

H' and $1/D$ are useful indices for quantifying diversity, but each has deficiencies in characterizing community structure. In the examples presented here, the two communities from the Hays data set were similarly diverse as shown by these diversity indices, regardless of how species were ordered. As stated previously, this is because of the nature of the formulas of H' and $1/D$. This result is not entirely surprising because Hopton and Choate (2002) determined the roadways were not a strong barrier to most of the small mammals at this site. Although there were minor differences in how species responded to the presence of roadways, roads did not isolate the small mammals. Thus, small mammals were free to move from one patch to another, resulting in similar species and similar diversities between sites. Hence, the study site likely consisted of a single small mammal community.

The diversity indices for the two communities from the Borneo data set were statistically different and the terrestrial community had higher index values than the arboreal community. One might expect the two communities to be composed of different species of small mammals because of the different traits that often accompany an arboreal existence (e.g., Gebo and Sargis 1994). However, that does not mean one community is necessarily more diverse than another community. Of course, Shannon's and Simpson's diversity indices for the two communities did not change when the species were reordered.

When the two communities from the Hays data set were arranged by decreasing rank abundance or phylogeny, there was not a difference between the observed FI values (although it was marginally non-significant when arranged by phylogeny; $P = 0.0541$). This

suggests that, structurally, the two communities are phylogenetically similar. When the two communities were arranged by increasing body mass, FI values for the two communities were significantly different (Table 3). The community sampled inside the median triangles had higher FI values than the community from the surrounding roadside. FI detected the difference resulting from a lack of individuals of the largest and smallest species on the triangles as compared with the roadside community.

Using the Borneo dataset, we show that although the terrestrial community is more diverse than the arboreal community, FI did not detect a difference between the two communities when ordered according to increasing body mass. This suggests that, according to the distribution of body mass, the two communities were similar. However, when species were arranged according to decreasing rank abundance or phylogenetic order, the arboreal community had significantly greater FI values compared to the terrestrial community. The greater FI value resulted from the arboreal community consisting of more species of sciurids.

As discussed earlier, the reason FI is more sensitive to subtle differences between communities in the above two examples is that it measures the slope between species proportions (i.e., difference in abundance between two adjacent species) and then adds the slopes to calculate the FI (Equations 3 & 4). Hence, when groups are reordered and compared between communities, the slopes can change and the structural differences between communities can be revealed.

We have shown that FI is sensitive to differences between communities that may not be detected by some of the more common indices, such as Shannon's and Simpson's diversity indices. For instance, a community that is composed of more ecologically dissimilar taxa is likely more diverse than one that is not (Purvis and Hector, 2000, Ricotta, 2007, Solow and Polasky, 1994). Often, Shannon's and Simpson's diversity indices cannot detect such differences, but FI can detect them. Thus, we believe the proposed Fisher Information index, in combination with established diversity indices, is a novel method for assessing and comparing community structure in ecosystems.

Taylor (1978) recognized that the effectiveness of any measure of diversity depends on how well it can differentiate minor differences between sites. With respect to community structure, communities are usually made up of more habitat specialists than generalists, and diversity is increased due to the addition of habitat specialists to communities (Kolasa and Li, 2003). Species and functional group richness are known to be critical components for ecosystem function and ecological resilience (Wittebolle et al., 2009). Community evenness has been shown to effect system dynamics, as well as the susceptibility of a system to invasions. Wittebolle et al. (2009) speculate that in communities that are more functionally redundant, if initial evenness is high, there is a greater probability that there are species in the community tolerant of perturbations. In contrast, if initial evenness is low and the species is dominated by one or a few species, the community will likely be resilient to perturbations only if the dominant species are tolerant to perturbations. Wittebolle et al. (2009) found that initial community evenness (i.e., community structure) is a key factor in maintaining the resilience of an ecosystem. For instance, if a community within a system is highly uneven or

there is dominance by a single or a few species, that system will be less resilient to perturbations.

An index based on Shannon [or Simpson] cannot completely detect the structure that may be embedded in an ecosystem (Brooks, 2003). FI, combined with Shannon or Simpson indices, captures information embodied in the structure of an ecosystem. Moreover, its use is not limited to the examples presented here. For instance, communities can be analyzed using FI to identify changes within a community through time, such as after a regime shift, or for comparing the trophic structure of two communities.

Classic ecological theory assumes that there is a balance of nature, for instance through carrying capacity, or through single-regime lakes (Buckland et al., 2005). Our current understanding of ecosystem dynamics tells us that nature is not so static, but rather, characterized by multiple regimes and non-linear dynamics (Gunderson and Holling, 2002). Thus, our goal should be to document changes in community structure over time, in order to provide the tools necessary for management to take appropriate actions (Diserud and Aagaard, 2002, Buckland et al., 2005). Biodiversity is being lost globally at accelerating rates (Watson et al., 2016). Thus, understanding the manner in which species self-organize into ecological communities (e.g., community structure) is of great importance for sustainability (Etienne and Olff, 2005). Further, the assessment and comparison of community structure is critical because the species in a community are assumed to exhibit self-organized interactions (Azovsky, 2009). For the reasons stated previously, the development of methodologies to compare and assess community structure is of increasing importance (Etienne and Olff, 2005).

5 Conclusion

It appears that no single diversity index is sufficient for characterization of biodiversity (Spanbauer et al., 2016), but FI could prove useful as an aid to some of the existing diversity indices, particularly if researchers are interested in assessing and comparing community structure. Thus, we suggest further research is warranted and provided the code for *R*, a free, open source computing platform (<http://www.r-project.org>). This will enable researchers to apply the technique to their own research questions and further explore the benefit FI can provide when examining community structure.

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Appendix 1.

Code to calculate Solow's randomization test for Shannon index, Simpson's Index, and Fisher Information with 10,000 replicates. The code is run in *R* and is used to calculate indices based on phylogenetic ordering in this example.

```
# calculate estimated p-value for difference in two communities based on
# species-abundance data using Solow's randomization test
filename <- "Borneo.phylogeny.txt"
# ordered by phylogeny and increasing body mass
# A = terrestrial
# B = arboreal
# number of replicates
nrep <- 10000
# set seed for random number generator
# sample (1000000, 1) = 183730
set.seed (183730)
# Shannon diversity index
shannon <- function (x)
{
  total <- sum (x)
  y <- x / total
  shannon <- sum (-y * log (y))
  return (shannon)
}
# Simpson's diversity index
simpson <- function (x)
{
  total <- sum (x)
  D <- sum (x*(x-1)) / (total*(total-1))
  invsimpson <- 1 / D
  return (invsimpson)
}
# Fisher's information statistic
fisher <- function (x)
{
  total <- sum (x)
  p <- x / total
  q <- sqrt (p)
  dq <- abs (diff (q))
  fisher <- 4 * sum (dq^2)
  return (fisher)
}
dat <- read.csv (filename, header=TRUE, strip.white=TRUE)
```

```

# separate the two samples
A <- dat$A[! is.na (dat$A)]
B <- dat$B[! is.na (dat$B)]
num <- ifelse (is.na (dat$A), dat$B, dat$A)
spp <- as.character(dat$Species)
# creates matrix containing species name and their ID number
species.names <- data.frame (spp=spp, num=num)
species.names <- unique (species.names)
nspp <- nrow (species.names)
# calculate observed difference statistics
pdfA <- table (sort (A))
pdfB <- table (sort (B))
shannonA <- shannon (pdfA)
shannonB <- shannon (pdfB)
dshannon.obs <- abs (shannonA - shannonB)
simpsonA <- simpson (pdfA)
simpsonB <- simpson (pdfB)
dsimpson.obs <- abs (simpsonA - simpsonB)
pdfA.fisher <- rep (0, nspp)
pdfB.fisher <- rep (0, nspp)
pdfA.fisher[as.integer(names(pdfA))] <- pdfA
pdfB.fisher[as.integer(names(pdfB))] <- pdfB
fisherA <- fisher (pdfA.fisher)
fisherB <- fisher (pdfB.fisher)
dfisher.obs <- abs (fisherA - fisherB)
# combine for tests
sampleC <- c (A, B)
# matrix to keep statistics for each replicate
stats <- matrix (0, nrow=nrep, ncol=3)
dimnames (stats) <-
list (seq(nrep), c("dshannon.sim", "dsimpson.sim", "dfisher.sim"))
# loop over replicates
for (i in 1:nrep)
{
# A sample
x <- sample (sampleC, length(A), replace=TRUE)
pdfA <- table (x)
pdfA.fisher <- rep (0, nspp)
pdfA.fisher[as.integer(names(pdfA))] <- pdfA
# B sample
x <- sample (sampleC, length(B), replace=TRUE)
pdfB <- table (x)
pdfB.fisher <- rep (0, nspp)
pdfB.fisher[as.integer(names(pdfB))] <- pdfB

```

```
# difference statistics
statA <- shannon (pdfA)
statB <- shannon (pdfB)
stats[i, "dshannon.sim"] <- abs (statA - statB)
statA <- simpson (pdfA)
statB <- simpson (pdfB)
stats[i, "dsimpson.sim"] <- abs (statA - statB)
statA <- fisher (pdfA.fisher)
statB <- fisher (pdfB.fisher)
stats[i, "dfisher.sim"] <- abs (statA - statB)
pvalue.shannon <- sum (stats[, "dshannon.sim"] > dshannon.obs) / nrep
pvalue.simpson <- sum (stats[, "dsimpson.sim"] > dsimpson.obs) / nrep
pvalue.fisher <- sum (stats[, "dfisher.sim"] > dfisher.obs) / nrep
```

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Figure 1.

Small mammal community from Hays dataset demonstrating Fisher Information is measuring the slope of the proportions. The slope of the line between each species is dependent on the order of species in the graph and will reveal additional information (i.e., community structure) about the community, based on this order.

Table 1

– Species richness and abundance data from Hopton and Choate (2002) for comparisons of community structure. Two communities (Median and Roadside) were compared by re-ordering the species sampled from each community. Species were ordered by rank abundance, increasing body mass, or phylogeny. The number under each ordering scheme corresponds to the order of species, with species ordered 1 through 10.

Species	Community		Order		
	Median	Roadside	Rank	Body Mass	Phylogeny
<i>Peromyscus maniculatus</i>	99	149	1	5	6
<i>Mus musculus</i>	39	70	2	4	8
<i>Microtus ochrogaster</i>	22	22	3	7	2
<i>Sigmodon hispidus</i>	5	11	4	9	7
<i>Reithrodontomys megalotis</i>	1	15	5	2	4
<i>Cryptotis parva</i>	1		6	1	10
<i>Blarina hylophaga</i>		1	7	3	9
<i>Microtus pennsylvanicus</i>		1	8	6	3
<i>Spermophilus tridecemlineatus</i>		1	9	8	1
<i>Neotoma floridana</i>		1	10	10	5
Total	167	271			

Table 2

Species richness and abundance data from Wells et al. (2004) for comparisons of community structure. Two communities (Terrestrial and Arboreal) were compared by re-ordering the species sampled from each community. Species were ordered by rank abundance, increasing body mass, or phylogeny. The number under each ordering scheme corresponds to the order of species, with species ordered 1 through 20.

Species	Community		Order		
	Terrestrial	Arboreal	Rank	Body Mass	Phylogeny
<i>Chiropodomys major</i>	2	34	1	1	12
<i>Maxomys whiteheadi</i>	16		2	3	17
<i>Tupaia minor</i>	4	8	3	6	3
<i>Niviventer cremoriventer</i>	6	6	4	8	18
<i>Maxomys surifer</i>	9		5	10	16
<i>Tupaia gracilis</i>	6		6	4	1
<i>Leopoldamys sabanus</i>	5	1	7	17	14
<i>Lenothrix canus</i>		6	8	12	13
<i>Sundasciurus hippurus</i>	3	2	9	16	10
<i>Sundasciurus lowii</i>	4		10	7	11
<i>Tupaia longipes</i>	4		11	11	2
<i>Tupaia tana</i>	3		12	15	4
<i>Maxomys baeodon</i>	2		13	5	15
<i>Sundasciurus brookei</i>	1	2	14	9	9
<i>Nycticebus coucang</i>	1	1	15	18	6
<i>Herpestes brachyurus</i>	1		16	19	20
<i>Trichys fasciculata</i>	1		17	20	19
<i>Ptilocercus lowii</i>		1	18	2	5
<i>Callosciurus notatus</i>		1	19	13	7
<i>Hylopetes spadiceus</i>		1	20	14	8
Total	68	63			

Table 3

Results of Shannon's diversity Index (H'), Simpson's diversity Index ($1/D$), and Fisher Information (FI) with three different orderings. Index = diversity index tested; Median = community sampled on vegetated triangles formed by exit and entrance ramps on the interstate highway; Roadside = community sampled on vegetated strips adjacent to interstate highway; Terrestrial = community sampled on ground in forest; Arboreal = community sampled in trees in forest; Difference = absolute value of the index of first community minus index of second community; leftmost P -value is estimated from resampling technique with seed set at 183730; rightmost P -value is from t -table based on Student's t -distribution; t = calculated t -statistic, df = degrees of freedom; t 0.05, (2), 399 or 35 = critical t -value at $\alpha = 0.5$, two-tailed, and 399 (Hays data) or 35 (Borneo data) degrees of freedom.

Hays Communities								
Rank Abundance								
Index	Median	Roadside	Difference	P-value	t	df	t _{0.05, (2), 399}	P-value
H'	1.0829	1.2553	0.1724	0.0689	0.2419	399.2124	1.966	> 0.05
1/D	2.3763	2.6449	0.2686	0.3004	0.8684	399.2124	2.160	> 0.05
FI	0.5915	0.6857	0.0942	0.5355				
Body Mass								
Index	Median	Roadside	Difference	P-value	t	df	t _{0.05, (2), 399}	P-value
H'	1.0829	1.2553	0.1724	0.0698	0.2419	399.2124	1.966	> 0.05
1/D	2.3763	2.6449	0.2686	0.3004	0.8684	399.2124	2.160	> 0.05
FI	4.9515	3.776	1.1755	0.0485				
Phylogeny								
Index	Median	Roadside	Difference	P-value	t	df	t _{0.05, (2), 399}	P-value
H'	1.0829	1.2553	0.1724	0.0698	0.2419	399.2124	1.966	> 0.05
1/D	2.3763	2.6449	0.2686	0.3004	0.8684	399.2124	2.160	> 0.05
FI	6.2413	4.8588	1.3825	0.0541				
Borneo Communities								
Rank Abundance								
Test	Terrestrial	Arboreal	Difference	P-value	t	df	t _{0.05, (2), 35}	P-value
H'	2.4594	1.5907	0.8687	0	3.2469	35.0133	2.030	< 0.05
1/D	10.2613	3.1449	7.1164	0.0037	61.2403	35.0133	2.060	< 0.05
FI	1.2327	3.7135	2.4808	0.0001				
Body Mass								
Test	Terrestrial	Arboreal	Difference	P-value	t	df	t _{0.05, (2), 35}	P-value

Hays Communities									
<i>H'</i>	2.4594	1.5907	0.8687	0	3.2469	35.0133	2.030	< 0.05	
<i>1/D</i>	10.2613	3.1449	7.1164	0.0037	61.2403	35.0133	2.060	< 0.05	
<i>F/I</i>	2.2296	3.9163	1.6867	0.0921					
Phylogeny									
Test	Terrestrial	Arboreal	Difference	<i>P</i> -value	<i>t</i>	<i>df</i>	$t_{0.05,(2),35}$	<i>P</i> -value	
<i>H'</i>	2.4594	1.5907	0.8687	0	3.2469	35.0133	2.030	< 0.05	
<i>1/D</i>	10.2613	3.1449	7.1164	0.0037	61.2403	35.0133	2.060	< 0.05	
<i>F/I</i>	1.3482	5.0607	3.7125	0.0001					