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Assessing biological dissimilarities between five forest communities



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Abstract

Background: Dissimilarity in community composition is one of the most fundamental and conspicuous features by which different forest ecosystems may be distinguished. Traditional estimates of community dissimilarity are based on differences in species incidence or abundance (e.g. the *Jaccard*, *Sørensen*, and *Bray-Curtis* dissimilarity indices). However, community dissimilarity is not only affected by differences in species incidence or abundance, but also by biological heterogeneities among species.

Methods: The objective of this study is to present a new measure of dissimilarity involving the biological heterogeneity among species. The “discriminating Avalanche” introduced in this study, is based on the taxonomic dissimilarity between tree species. The application is demonstrated using observations from five stem-mapped forest plots in China and Mexico. We compared three traditional community dissimilarity indices (*Jaccard*, *Sørensen*, and *Bray-Curtis*) with the “discriminating Avalanche” index, which incorporates information, not only about species frequencies, but also about their taxonomic hierarchies.

Results: Different patterns emerged for different measures of community dissimilarity. Compared with the traditional approaches, the discriminating Avalanche values showed a more realistic estimate of community dissimilarities, indicating a greater similarity among communities when species were closely related.

Conclusions: Traditional approaches for assessing community dissimilarity disregard the taxonomic hierarchy. In the traditional analysis, the dissimilarity between *Pinus cooperi* and *Pinus durangensis* would be the same as the dissimilarity between *P. cooperi* and *Arbutus arizonica*. The dissimilarity Avalanche dissimilarity between *P. cooperi* and *P. durangensis* is considerably lower than the dissimilarity between *P. cooperi* and *A. arizonica*, because the taxonomic hierarchies are incorporated. Therefore, the discriminating Avalanche is a more realistic measure of community dissimilarity. This main result of our study may contribute to improved characterization of community dissimilarities.

Keywords: Avalanche index, Biological distance, Community dissimilarity, Forest community, New approach

Background

Dissimilarity in community composition is one of the most conspicuous features of forest ecosystems (Jost et al. 2011). Assessing compositional differences between forest communities is an important issue for several reasons. Dissimilarities between forest communities can reveal certain mechanisms that generate and maintain forest biodiversity and specific habitat effects that shape

forest composition and structure (Socolar et al. 2016). Assessing dissimilarities between forest communities is essential for evaluating species invasions, changes caused by selective tree harvesting, or effects of climate change on species composition. In addition, effective measures of community dissimilarity may contribute to more meaningful classifications of forest vegetation (Wehenkel et al. 2014).

Jaccard (1900) was probably the first who proposed a method for measuring the degree of community similarity and dissimilarity based on the number of species shared by two communities and the number of species

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unique to each of them. Two additional indices were subsequently proposed to estimate the difference between communities (Sørensen 1948; Bray and Curtis 1957). The Jaccard and Sørensen indices are using species presence/absence data. The Bray-Curtis index, a modified version of the Sørensen index, includes species abundances (Chao et al. 2005). These three indices have become the most widely used measures for assessing community similarity or dissimilarity in community ecology (Anderson et al. 2006). In addition, several other species incidence- or abundance-based indices have been developed (Chao et al. 2005; Legendre and Legendre 2012). Examples are the Chi-square distance index (Fenelon and Lebart 1971), the Canberra index (Lance and Williams 1967; Stephenson et al. 1972), and the Morisita-Horn index (Magurran 2004).

These indices have been widely used in forest ecology, and they contribute substantially to the understanding of community dissimilarity. However, community dissimilarity is not only affected by differences in species abundance or incidence, but also by the biological heterogeneity among species (Clarke and Warwick 1998, 2001). Accordingly, the purpose of this study is to evaluate a new measure of community dissimilarity that incorporates both the information of species frequencies and the biological heterogeneity among species. The new approach is based on the “Avalanche” index proposed by Ganeshiah et al. (1997) and Ganeshiah and Shaanker (2000). The biological dissimilarity among species can be calculated using species taxonomic, genetic or morphometric information.

Data and methods

We are using observations from five 1-ha (100 m × 100 m) forest plots, three from Mexico and two from China, to demonstrate the new approach (Fig. 1).

Observational field plots

The three Mexican plots are located in the communal forests of Durango (22°20′–26°47′ N; 103°46′–107°12′ W), which occupy about 23% of the area of Sierra Madre Occidental. The elevation above sea level varies between 363 and 3200 m (average 2264 m). The precipitation ranges from 443 to 1452 mm, with an annual average of 917 mm, while the mean annual temperature varies from 8.2 to 26.2 °C, with an annual average of 13.3 °C (González-Elizondo et al. 2012; Silva-Flores et al. 2014). The predominant forest types are uneven-aged, semi-natural forests, which are dominated by *Pinus* spp. and *Quercus* spp., and often in mixture with *Arbutus* spp., *Juniperus* spp., and *Pseudotsuga menziesii* (Silva-Flores et al. 2014; Lujan-Soto et al. 2015). In Durango, many local residents depend on the forests for their livelihood. But despite the high biological, cultural and socio-economic importance of the Sierra Madre Occidental, these forests are not very well known. Details about the history of these unique ecosystems may be found in Burgos and Villa (1974), and Corral-Rivas et al. (2015).

The three forests where the plots are located, have been managed selectively by local communities known as *Ejidors*. Previous commercial harvests were based on maintaining an inverse J-shaped diameter class distribution (Virgilietti and Buongiorno 1997). The sites have been protected for many years, and are located in the vicinity of a National Park. The exact treatment histories are not known. The permanent field plots, named after the local *Ejidors* “La Victoria”, “San Esteban” and “Mil Diez”, are located in the region of El Salto, Pueblo Nuevo, Durango. All the woody stems in the three plots with DBH ≥ 5 cm were identified, measured and stem-mapped. A total of 2041 individual trees belonging to eleven species, four genera, and four families are included in the three plots. The main species in terms of

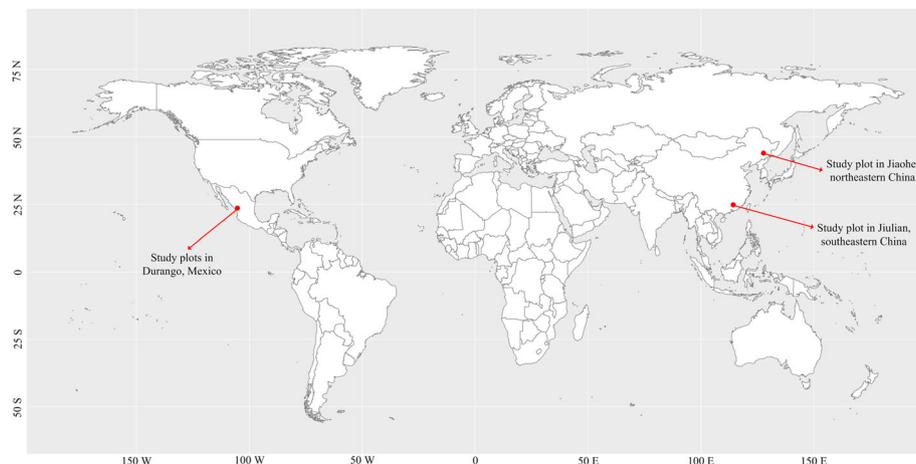


Fig. 1 World map showing the location of the observational forest plots in China and Mexico

basal area are *Pinus cooperi*, *Quercus sideroxylla*, and *Pinus durangensis*.

The two plots from China are from unmanaged forests. One plot is located in a temperate broad-leaved Korean pine (*Pinus koraiensis*) mixed forest in Jiaohe Forest Experimental Zone (43°51′–44°05′ N, 127°35′–127°51′ E), in Jilin Province, northeastern China (hereafter referred to as “Jiaohe”). The other plot is situated in a subtropical evergreen broad-leaved forest in Jiulian Mountain National Natural Reserve (24°29′–24°39′ N; 114°22′–114°32′ E), in Jiangxi Province, southeastern China (hereafter “Jiulian”). The mean annual temperature in Jiaohe is 3.8 °C, with average monthly temperature ranges from –18.6 °C to 21.7 °C, while the mean annual temperature in Jiulian is 17.4 °C, with average monthly temperature ranges from 6.8 °C to 24.4 °C. The mean annual precipitation is 696 mm (Jiaohe) and 2156 mm (Jiulian), respectively (Hao et al. 2018). There are 675 individuals belonging to 28 species, 18 genera and 13 families in Jiaohe plots, and 1060 individuals belonging to 112 species, 68 genera and 38 families in the Jiulian plots. Details of the five research plots are presented in Table 1.

Dissimilarity between species

The biological dissimilarity (or “distance”) between species refers to the difference between species in terms of certain genetic or morphological characteristics (Faith 1992; Ganeshiaiah et al. 1997; Clarke and Warwick 1998). The biological dissimilarity can be assessed based on plant traits (Ganeshiaiah et al. 1997), phylogeny (Faith 1992), or taxonomy (Clarke and Warwick 1998, 1999). In this study, we choose to calculate the biological dissimilarity between species using the information of a Linnean taxonomy. Measuring the taxonomic distance is relatively straightforward, compared with the use of more complex plant traits or phylogeny. The taxonomic distances are estimated based on a table of classification which includes the five taxonomic levels (species, genus, family, order, and group).

The standard botanical nomenclature follows *The Plant List* (TPL, www.theplantlist.org), which represents an internationally accepted standard database for plant nomenclature. The taxonomic information is extracted from the APG IV classification system (Angiosperm

Phylogeny Group 2016) and Christenhusz et al. (2011), for Angiosperms and Gymnosperms, respectively. The distances between species are scaled such that the longest path length between taxa is 1. For example, the distance would be 1 if two individuals belong to different taxonomic groups (*Angiosperms* and *Gymnosperms*). The distance would be 0.8 if two individuals belong to different orders, but share the same group (e.g. *Pinales* and *Fagales*). By that analogy, the distance would be 0.2 for two individuals that belong to different species but share the same genus. The normalized distances between two individuals that differ at different levels within the taxonomic hierarchy are presented in Table 2.

The Jaccard, Sørensen and Bray-Curtis indices

The Jaccard, Sørensen, and Bray-Curtis indices are presented in Table 3 for easy reference. These indices are well known and widely applied, especially in the assessment of community dissimilarity.

The simple, complete, discriminating and plain avalanche

The “Avalanche index” (Ganeshiaiah et al. 1997; Ganeshiaiah and Shaanker 2000) represents a generalization of the phylogenetic diversity index proposed by Faith (1992). Which broadens the distance component to allow for any quantitative information that is biologically informative (not just phylogeny), and that can measure the proximity of any given pair of species (Talents et al. 2005). If only species incidence data are available, the simple Avalanche index (sA) is defined as follows:

$$sA = \sum_{i=1}^n \sum_{j=1}^n d_{ij} \quad (1)$$

where n is the number of species and d_{ij} is the biological distance between species i and j . sA can be standardized by normalizing the d_{ij} and dividing the sA by $n(n-1)$. The result is a value in the interval [0,1]. This is a great advantage when compared with the Shannon index (or Hill numbers) of species diversity. If species abundance data are available, the complete Avalanche (cA), which estimates the biodiversity within a community, can be used:

Table 1 Basic information of the five forest plots used in the analyses

Plots	Altitude (m)	Slope (%)	Species richness	Stems per ha	Mean DBH (cm)	Mean height (m)	Basal area (m ² ·ha ⁻¹)
La Victoria	2711	3	10	587	21.03	13.58	26.09
San Esteban	2168	15	8	753	19.27	11.77	28.08
Mil Diez	2601	10	7	701	19.64	13.68	26.96
Jiaohe	766	20	28	675	19.41	12.16	33.44
Jiulian	668	19	112	1060	16.42	11.14	41.29

Table 2 Normalized distances between two individuals that differ at different levels within the taxonomic hierarchy

Individuals differ by different taxonomic hierarchy	Normalized distance
Species	0.2
Genus	0.4
Family	0.6
Order	0.8
Group	1.0

$$cA = \sum_{i=1}^n \sum_{j=1}^n p_i d_{ij} p_j \tag{2}$$

where n is the number of species and d_{ij} is the taxonomic, phylogenetic or trait distance between species i and j ; p_i and p_j are the relative frequencies of species i and j in the community. In addition, p_i and p_j can also be the relative basal area or biomass or other weights of species i and j . Based on these original “Avalanches”, we present a new measure called “discriminating Avalanche”, which can be used to quantify the biological dissimilarity (or distance) between two communities. The discriminating Avalanche (dA) is based on species frequencies and some measure of biological distance among species:

$$dA = \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \Delta_i^{a,b} d_{ij} \Delta_j^{a,b} \tag{3}$$

where $\Delta_i^{a,b}$ refers to the absolute difference between the frequencies of species i in plots a and b ($\Delta_i^{a,b} = |p_i^a - p_i^b|$, p_i^a and p_i^b are the relative frequencies of species i in plots a and b), and $\Delta_j^{a,b}$ is the equivalent for species j . If the maximum d_{ij} is known, then the d_{ij} can be normalized by dividing the actual values of d_{ij} by the maximum value of the d_{ij} , and dA will thus assume values in the interval [0, 1]. If we disregard the biological distance among species (as in the case of Jaccard, Sørensen, and Bray-Curtis) but only emphasize the differences in species frequency, we obtain the “Plain Avalanche” (pA):

$$pA = \frac{1}{2} \sum_{i=1}^n \sum_{j=1}^n \Delta_i^{a,b} \Delta_j^{a,b} \tag{4}$$

The Plain Avalanche distances are expected to be greater than the discriminating Avalanche distances in situations where many individuals differ by species but share the same genus or family.

Results

Based on the discriminating Avalanche (dA) the community distances among forests with species taxonomic information are obtained (Fig. 2). We simultaneously calculated the Jaccard, Sørensen, Bray-Curtis, and Plain Avalanche (pA) community dissimilarity indices, and found different patterns for different measures of dissimilarity (Fig. 3; Additional file 1: Table S1). Compared with the traditional measures, the discriminating Avalanche values showed relatively low distances, i.e. a greater similarity among plots, as closer relations among species are revealed by dA.

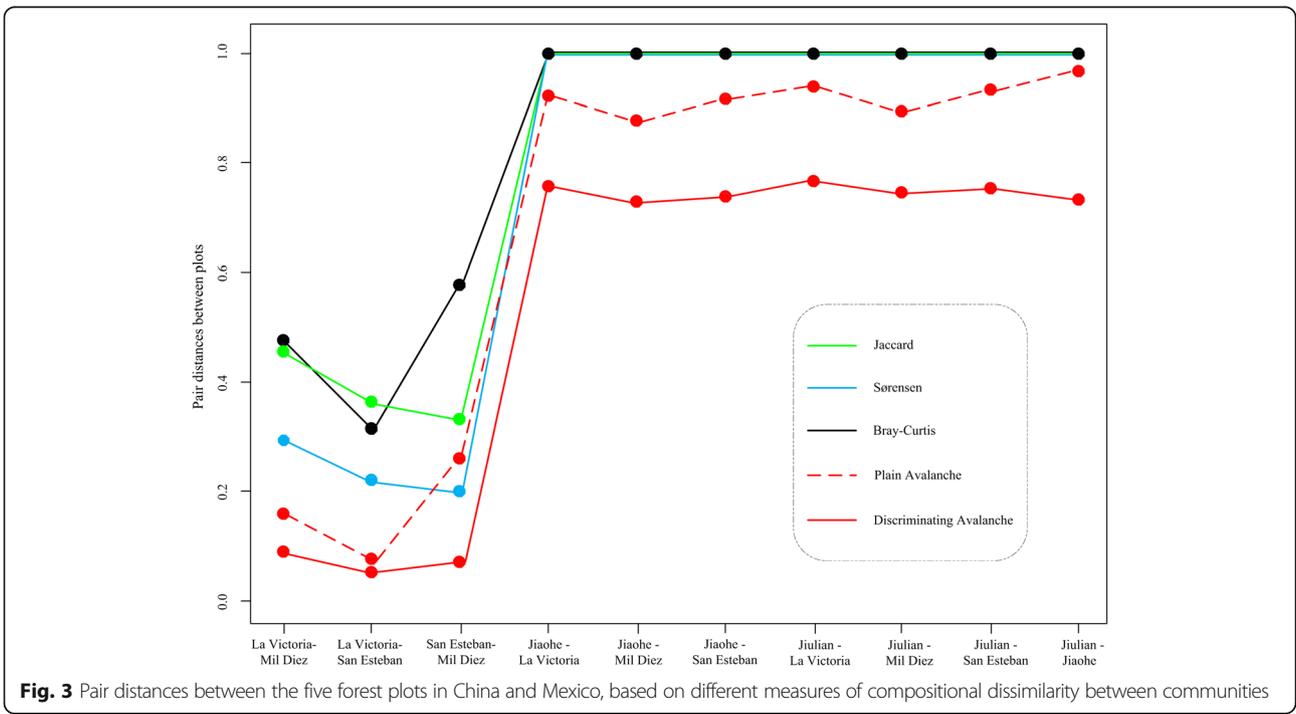
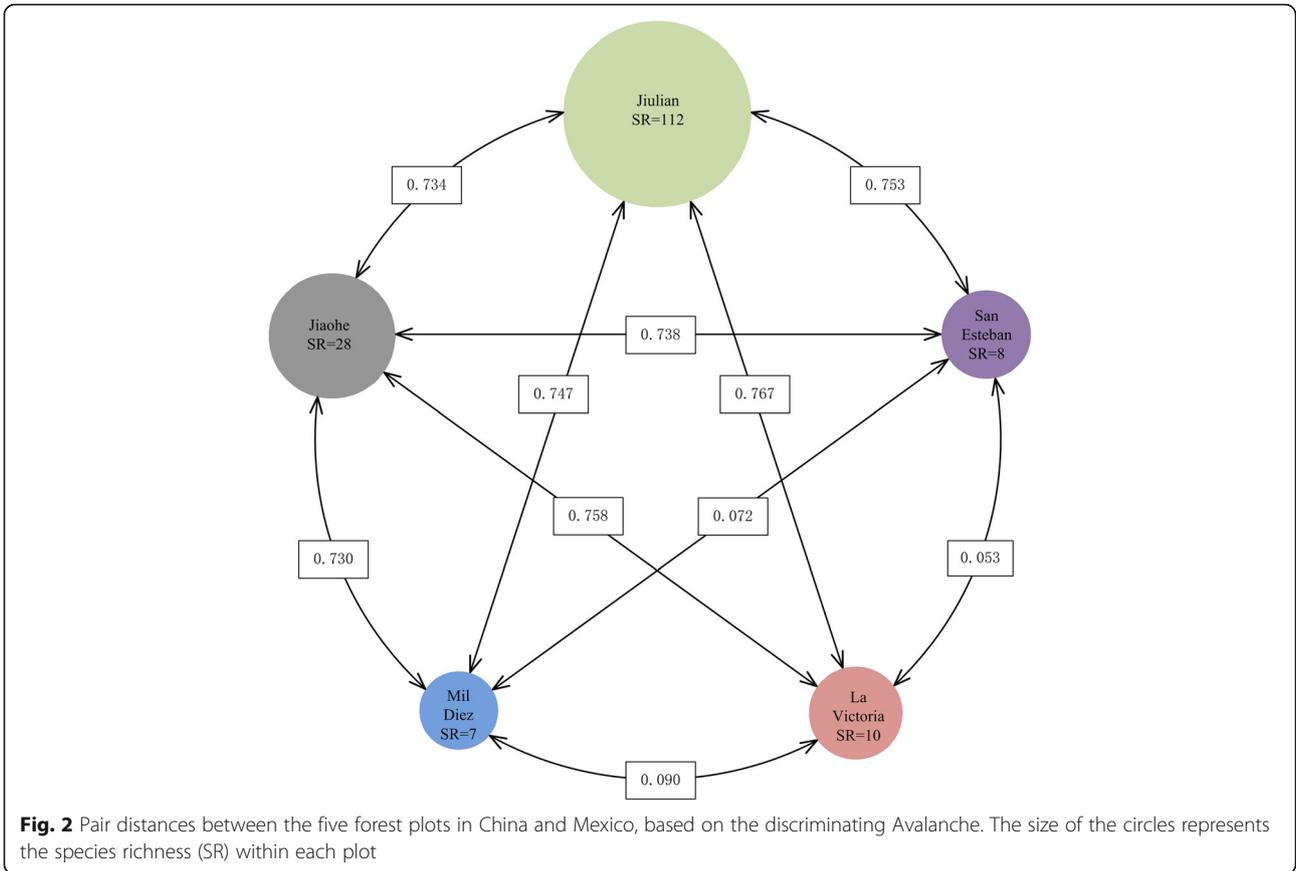
With regard to the three forest plots in Mexico, the Jaccard and Sørensen dissimilarities exhibit similar tendencies: a closer distance between plots San Esteban and Mil Diez, and a relatively greater distance between La Victoria and Mil Diez. The pA distances exhibit a tendency which is similar to Bray-Curtis: a closer distance between La Victoria and San Esteban, and a greater distance between San Esteban and Mil Diez. The dA distances are different from all others: a closer distance between La Victoria and San Esteban, and a greater distance between La Victoria and Mil Diez (Fig. 3; Additional file 1: Table S1). When there are no shared species between plots, the Jaccard, Sørensen, and Bray-Curtis distances are both 1, i.e. the maximum value of these indices. The pA and dA distances, although there are no shared species in the forest plots in China and Mexico, do not reach the maximum value. These results will be discussed in detail in the discussion section.

Discussion

Assessing the difference among communities has become a central issue in community ecology (Chao et al. 2005; Legendre and Cáceres 2013). In this study, we presented a new taxonomy-based approach, which is easy

Table 3 Details of the Jaccard, Sørensen, and Bray-Curtis dissimilarity indices

Dissimilarity	Equation	Details
Jaccard index	$\frac{B+C}{A+B+C}$	A represents the number of species shared by two communities, B and C are the number of species unique to each of the two communities
Sørensen index	$\frac{B+C}{2A+B+C}$	
Bray-Curtis index	$\frac{\sum_{i=1}^n p_i^a - p_i^b }{\sum_{i=1}^n (p_i^a + p_i^b)}$	n is the number of species; p_i^a and p_i^b are the relative frequencies of species i in plots a and b



to implement, and which will bring new information compared to traditional approaches of assessing community dissimilarity, and can be applied flexibly in any pair of communities with any species richness.

Measures of community dissimilarity

Community “similarity” or “dissimilarity” is a qualitative human construct which has no precise mathematical definition. Nevertheless, measuring community dissimilarity should rely on some quantitative measure that can be devised for a specific purpose (Chao et al. 2005). Dissimilarity means “not the same”. When we state that two forest communities are the same, what we are really doing is to neglect those differences that we choose to ignore. Therefore, although numerous measures have been published, the development of new measures for quantifying community dissimilarity more accurately, more comprehensively and objectively remains a priority in community ecology (Chao et al. 2005).

One property that any new measure should have is that it should not be redundant with existing indices. Therefore, the new measure is compared with the well known Jaccard, Sørensen, and Bray-Curtis dissimilarity indices. The patterns of biological dissimilarity presented in Fig. 3 differ considerably. Based on these differences, the five measures of dissimilarity are assigned to three groups. The first group which we call the Species Presence-Absence group, includes the Jaccard and Sørensen dissimilarities. The Jaccard and Sørensen are based solely on species incidence (presence-absence) data, i.e. the number of species shared by two plots and the number of species unique to each. It is not surprising that Jaccard and Sørensen exhibit similar tendencies (e.g. a closer distance between plots San Esteban - Mil Diez, a relatively longer distance between plots La Victoria - Mil Diez, and the longest distance when two plots have no shared species). Six species are shared by San Esteban and Mil Diez, while only three species are unique to each of these two communities. The dissimilarity between the two plots is relatively small because the focus is only on species incidence. Jaccard calculates the unique (unshared) species as a proportion of the total number of species recorded in the two communities, while Sørensen gives double weight to the shared species (Table 3). The Sørensen dissimilarity is thus closely related to Jaccard, and always has a lower value than Jaccard.

The second group which we call the Species-Abundance group, includes the Bray-Curtis and Plain Avalanche dissimilarities. Both are calculated using the species abundance data. Bray-Curtis and Plain Avalanche dissimilarities exhibit a similar tendency (e.g. a closer distance between La Victoria - San Esteban, and a greater distance between San Esteban - Mil Diez). The

results seem to contradict the Presence-Absence group. Although there are six species shared by plots San Esteban and Mil Diez, the difference in the species frequencies is great resulting in higher dissimilarities. The Bray-Curtis and Plain Avalanche dissimilarities are based on the same information: the absolute difference on species frequencies (Table 3). However, there are differences between them: Bray-Curtis is calculated as the sum of absolute difference for all species ($\sum_{i=1}^n |p_i^a - p_i^b|$ or $\frac{1}{2} \sum_{j=1}^n (\Delta_j^{a,b})$), where $\Delta_j^{a,b} = |p_j^a - p_j^b|$, while the Plain Avalanche is calculated as the sum of products of pair-frequency differences for all species ($\sum_{i=1}^n \sum_{j=1}^n (\Delta_i^{a,b} \Delta_j^{a,b})$).

Compared with the Plain Avalanche, the discriminating Avalanche gives lower distances, i.e. a greater similarity among plots in these particular communities. This is due to the fact that in the Plain Avalanche, each species is treated as an entity that is different from another species. For example, the dissimilarity between *P. cooperi* and *P. durangensis* would be the same as the dissimilarity between *P. cooperi* and *A. arizonica*. However, in the discriminating Avalanche, the dissimilarity between *P. cooperi* and *P. durangensis* is considerably lower than the dissimilarity between *P. cooperi* and *A. arizonica*, because the taxonomic hierarchies are incorporated.

The maximum and minimum values of Jaccard, Sørensen, and Bray-Curtis are 1 (no shared species) and 0 (the same species composition), respectively. The minimum value of the discriminating Avalanche and the Plain Avalanche is 0 (the same species composition), while the maximum value is $(1 - \frac{1}{n})$, where n is the total number of species recorded in the two communities ($n \geq 2$; refer to the the mathematics theorem *inequality of arithmetic and geometric means*). Therefore the maximum value depends on the number of species. For example, if there are 10 species recorded in the two communities, the maximum value will be $(1 - \frac{1}{10} = 0.9)$; if there are 100 species, the maximum value will be $(1 - \frac{1}{100} = 0.99)$. For an infinite number of species, the value would be ~ 1 . The maximum value of dA is thus hard to be achieved in practice, even if there is no shared tree species between communities. We employed forest plots from China and Mexico to explain this property. In our example the forests in China and Mexico have almost no shared species. Jaccard, Sørensen, and Bray-Curtis therefore both give the maximum pairwise dissimilarities (Fig. 3). However, from a more evolutionary perspective, the regions are not totally and equally dissimilar and can be compared in terms of their relative taxonomic similarity. Therefore, the discriminating Avalanche is a more realistic measure of community dissimilarity.

Future work: estimating biological distances based on optimization

This study has shown that the Avalanche approach has the potential to be applied in discriminating among forest communities. Instead of using the Avalanche approach for assessing biological distances, the transportation model of linear programming may also be suitable for evaluating the biological distance between forest communities, based on the objective to minimize the “cost” of transforming community i into community j :

$$\min \rightarrow Z = \sum_i^m \sum_j^n \text{distance}_{ij} \cdot X_{ij} \quad (5)$$

where the distance_{ij} is some measure of the biological distance between species i and j . The X_{ij} are the numbers (or relative proportions) of the different species in communities i and j . The constraints would be the numbers (or relative proportions) of the different species in communities i and j :

$$\sum_j^n X_{ij} \leq \text{available}_i \text{ and } \sum_i^m X_{ij} \geq \text{required}_j \quad (6)$$

The potential of this approach will be evaluated in future studies.

Conclusions

This study presents a new method for estimating compositional dissimilarities (distances) between forest communities. Estimates of the biological “distance” are based on the Avalanche concept, using a simple taxonomic hierarchy and species frequencies. To increase the contrast and interpretation of this new approach, compositional dissimilarities of forest communities are also assessed using three more traditional approaches, the Jaccard, Sørensen, and Bray-Curtis community dissimilarity indices. The results suggest that the discriminating Avalanche approach is not redundant but complementary and possibly more meaningful than the existing approaches. Such “distance” estimates could reveal the degree of biological relatedness of forest ecosystems in different regions of the world, estimate the effects of habitat heterogeneity on community composition and diversity, and improve an assessment of the degree of species invasion or anthropogenic disturbance with reference to an assumed potential natural vegetation.

Additional file

Additional file 1: Table S1. Pair distances between the five forest plots in China and Mexico, based on different measures of compositional dissimilarity between communities (DOCX 21 kb)

Abbreviations

APG IV: Angiosperm phylogeny group IV; cA: Complete Avalanche; dA: Discriminating Avalanche; DBH: Diameter at breast height; pA: Plain Avalanche; sA: Simple Avalanche; TPL: The Plant List

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Authors' contributions

MH, CZ and KG: designed the study, performed data analyses and wrote the manuscript; JJCR, MGNM, CZ and XZ: created the database of forest plots; MSGE and KNG: provided comments and other technical support. All authors discussed the results and commented on the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Please contact the corresponding author for data requests.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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