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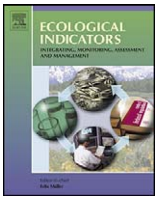

Measuring changes in taxonomic dissimilarity following species introductions and extirpations

Sébastien Villéger[a,b,*], Sébastien Brosse[a,b]

[a] CNRS, UPS, ENFA, UMR5174 EDB (Laboratoire Évolution et Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse, France
[b] Université de Toulouse, UMR5174 EDB, F-31062 Toulouse, France

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ABSTRACT

Species extirpation and non-native species introduction induce changes in compositional dissimilarity among communities. This major component of the current biodiversity crisis has been measured using different metrics since a methodological consensus is still lacking. Here, we provide a consensual framework to assess and discuss the changes in taxonomic dissimilarity.

Using a complete mathematical formalism of how extirpation and introduction processes affect changes in taxonomic dissimilarity, we compare the ability of the two most commonly used indices (Jaccard's and beta-sim) to detect the effects of these changes in species composition and richness. Simulations showed that the two indices indicate opposite direction of changes in more than 14% of the cases studied and that in most of the remaining cases the two indices show a discrepancy of more than 10%.

By returning to the definition of the dissimilarity concept we demonstrate that the Jaccard index is the most appropriate to measure changes in taxonomic dissimilarity whereas the beta-sim index only measures species turnover. Finally, the changes observed in Jaccard's dissimilarity can be decomposed into changes in taxonomic turnover and changes in taxonomic nestedness. Under the context of global change, the framework we propose will be useful as a toolbox to measure and predict human impact on biodiversity.

1. Introduction

Human activities impact both the abiotic and biotic components of all the ecosystems on Earth (Vitousek et al., 1997; Ellis et al., 2010). The resulting changes in species richness, from local habitats to continents, have been widely studied for several decades (e.g. Leprieur et al., 2008). However, biodiversity is a multifaceted concept that goes further than simply species richness (Purvis and Hector, 2000). Indeed, besides the diversity of a species assemblage (i.e. alpha diversity) a complementary facet is the dissimilarity among species assemblages (i.e. beta-diversity). For more than a decade now, changes in dissimilarity among species assemblages have been studied in the context of the current biodiversity crisis under the term of biotic homogenization (McKinney and Lockwood, 1999; Olden and Rooney, 2006). Taxonomic homogenization describes the increase in biological similarity among species assemblages after extirpation and/or introduction have modified their composition (McKinney and Lockwood, 1999; Olden and Poff, 2004). Indeed, non-native species often belong to a small pool of species of economic interest while extirpated native species often had a small geographic range (Blackburn and Cassey, 2007; Blanchet et al., 2010). Therefore, the loss of unique species and the gain of the same species in numerous assemblages contribute to an increasing similarity in species composition. However, while the emphasis is often put on taxonomic homogenization, the opposite trend called taxonomic differentiation is also a possible outcome of human activities, for example when different non-native species are introduced (e.g. Shaw et al., 2010).

Detecting and quantifying taxonomic homogenization (or differentiation) requires assessing temporal variation of taxonomic dissimilarity among a set of communities. Of the several indices measuring the taxonomic dissimilarity between two communities based on their species composition, the Jaccard dissimilarity index (Jaccard, 1912) has been the most frequently used (e.g. Rahel, 2000; Olden and Poff, 2003; La Sorte and McKinney, 2006; Olden and Rooney, 2006; Cassey et al., 2007; La Sorte and McKinney, 2007), but several other studies (e.g. La Sorte et al., 2007, 2008; Winter et al., 2009; Luck and Smallbone, 2011) have used the beta-sim index (Lennon et al., 2001). Given that comparison of dissimilarity changes among diverse regions or ecosystems requires a unique and comprehensive metric, there is an urgent need for a consensual framework to study taxonomic homogenization. In this aim,

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* Corresponding author at: Laboratoire Evolution et Diversité Biologique (UMR 5174), Université Paul Sabatier, 118 Route de Narbonne, 31062 Toulouse Cedex 4, France. Tel.: +33 561556747; fax: +33 561557327.
E-mail address: sebastien.villeger@univ-tlse3.fr (S. Villéger).

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we first formalized how the different types of species extirpations and introductions modify community dissimilarity. We then used simulations and examples to compare the relevance of Jaccard's and beta-sim indices to measure changes in dissimilarity and we finally propose a framework to accurately assess and discuss changes in dissimilarity.

2. A new formalism to assess changes in community dissimilarity

Here, we present a framework to study the effects of species extirpation and introduction on taxonomic dissimilarity between an "historical" and a "current" situation. This terminology refers to classic study cases, which aim at comparing species communities before and after human activities have affected their composition through species extirpations and/or introductions. Nevertheless, studying taxonomic dissimilarity changes could be done more generally between any reference situation and a later period, observed or even simulated under relevant scenarios.

2.1. Historical situation

Let consider two communities with respective historical compositions such that: a species were shared by the two communities while b and c were present only in communities I and II respectively (Fig. 1). The total number of species present in the two communities was $a+b+c$ and species richness of the two communities was $S_{\mathrm{I}} = a + b$ and $S_{\mathrm{II}} = a + c$, respectively.

As species richness has to be strictly positive (otherwise the community does not exist), this implies the following mathematical condition:

$$\begin{cases} a+b>0 \\ a+c>0 \end{cases} \Leftrightarrow (b \neq 0 \quad \text{and} \quad c \neq 0) \quad \text{or} \quad a \neq 0. \tag{1}$$

2.2. Introduction of non-native species and/or extirpation of native ones

Let now consider the changes in the species composition of these two communities due to extirpation of native species historically present and/or introduction of non-native species (Fig. 1a):

- y and z non-native species have been respectively introduced in communities I and II only.
- x non-native species have been introduced in both community I and II.
- v species have been translocated from community I to community II where historically they did not occur while for w species the opposite happened.
- i species that historically occurred in both community I and II have been extirpated from these two communities.
- j and k species that historically occurred in both community I and II have been extirpated only from communities II and I, respectively.
- m and n native species present historically only in community I and II respectively, have been extirpated.
- t species have been extirpated from community I but were introduced in community II where they historically did not occur and u species underwent the opposite transfer.

This exhaustive model is an extension of the conceptual model presented by Olden and Poff (2003) which detailed the 14 scenarios accounting for bilateral/unilateral modes of extinction and/or introduction, and whether the species extirpated/introduced were the same or not for the two communities. The formalism presented here details further the extinction and introduction patterns and allows mixed effects. For instance among the non-native species introduced, some are introduced in both communities (x) while others are introduced only in one community (y, z). Additionally some non-native species did not occur historically in the focal communities (x, y, z) while others have been translocated from one focal community to the other one (t, u, v, w). Some situations such as those quantified by t and u components may be rare in nature, but they can happen for example in the case of ex situ conservation of threatened endemic species (Minckley, 1995; Fischer and Lindenmayer, 2000).

2.3. Change in the number of species shared by the communities or not

To summarize the global effect of extirpation and introduction, let us consider the difference between the number of non-native species introduced and the number of native species that have been extirpated from the common and the two unique pools of species (Fig. 1b).

This difference will be noted e for the number of species shared by the two communities, and f and g for the number of species present only in communities I and II, respectively.

$$\begin{cases} e = x - i - j - k + v + w \\ f = y + j + u - m - v - t \\ g = z + k + t - n - w - u \end{cases}$$

e, f and g are negative when the number of species lost exceeds the number of non-native species gained.

Species richness in communities I and II are now $S'_{\mathrm{I}} = a + b + e + f$ and $S'_{\mathrm{II}} = a + c + e + g$, respectively. Thus, as the maximum number of species extirpated is determined by the number of species historically shared or not and as species richness has to be strictly positive the following conditions are met:

$$\begin{cases} e \geq -a \\ f \geq -b \\ g \geq -c \\ a+b+e+f>0 \\ a+c+e+g>0 \end{cases} \tag{2}$$

2.4. Measuring changes in dissimilarity due to species introductions and extirpations

According to the notation presented above (Fig. 1), the historical dissimilarity measured with the Jaccard index (Jaccard, 1912) (β_J) is: $\beta_J = (b+c)/(a+b+c)$, and thus ranges from 0 when $b=c=0$ (i.e. the two communities have an identical species composition) to 1 when $a=0$ (i.e. the two communities have a totally different species composition).

The beta-sim index (Lennon et al., 2001) for the historical situation (β_{sim}) is $\beta_{\mathrm{sim}} = \min(b, c)/(a + \min(b, c))$, and ranges from 0 when $\min(b,c)=0$ (i.e. one of the communities is a sub-sample of the other) to 1 when $a=0$ (i.e. the two communities have totally different species compositions). For simplicity, we propose to consider that $b \geq c$ and thus that $\beta_{\mathrm{sim}} = c/(a+c)$.

According to the notation in Fig. 1b, the current (i.e. after species extirpations and/or introductions occurred) number of species shared by the two communities is $a+e$ and the number of species present only in communities I and II are respectively $b+f$ and $c+g$.

Thus, current Jaccard's dissimilarity (β_J') between the two communities equals:

$$\beta_J' = \frac{b+f+c+g}{a+b+c+e+f+g}.$$