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

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.

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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,

* 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).

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 $S_I = a + b$ and $S_{II} = a + c$, respectively.

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

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

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 $S_I' = a + b + e + f$ and $S_{II}' = a + c + e + g$, 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:

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

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 $\beta_{sim} = \min(b, c)/(a + \min(b, c))$, 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 $\beta_{sim} = c/(a + c)$.

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:

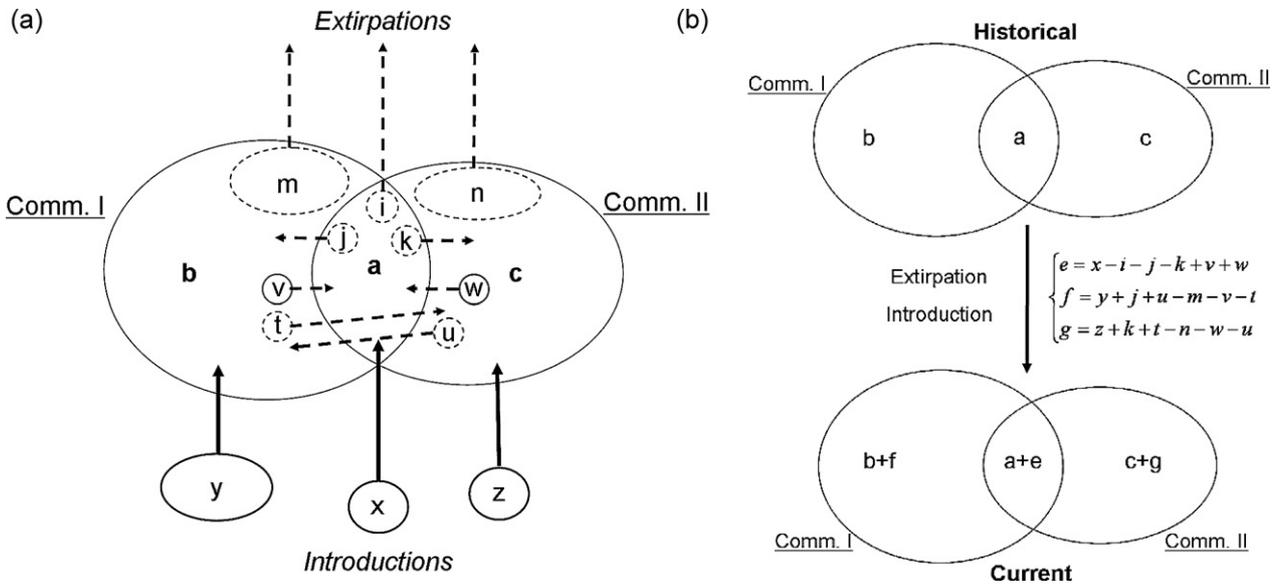$$\beta_J' = \frac{b + f + c + g}{a + b + c + e + f + g}.$$

Fig. 1. Conceptual framework of how species extirpation and introduction affect the taxonomic dissimilarity between two communities. (a) Schematic representation of the taxonomic dissimilarity between two communities. Species pools from the two communities are represented by the two ovals, their intersection symbolizing the species shared by the two communities. Letters represent the number of species initially present (a–c), introduced (t–z) or extirpated (i–n) from the communities. For further details, see main text. (b) Change in taxonomic dissimilarity from an "historical" to a "current" situation following species introductions and extirpations. Note that these terms are used for convenience. Comparisons between two past periods or between current situation and future simulated communities are also possible. Letters e, f and g represent changes in the number of species shared by the two communities or not after changes in species composition.

Consequently, change in Jaccard's dissimilarity from the historical to the current situation ($\delta\beta_J$) is:

$$\delta\beta_J = \beta'_J - \beta_J$$

$$\delta\beta_J = \frac{b+c+f+g}{a+b+c+e+f+g} - \frac{b+c}{a+b+c}$$

(3)

$$\delta\beta_J = \frac{a \times (f+g) - e \times (b+c)}{(a+b+c+e+f+g) \times (a+b+c)}$$

The beta-sim index for the current situation (β_{sim}') equals:

$$\beta'_{sim} = \frac{\min(b+f, c+g)}{(a+e) + \min(b+f, c+g)}.$$

To detail changes in the beta-sim index ($\delta\beta_{sim} = \beta_{sim}' - \beta_{sim}$) there are thus two cases to consider:

if $b+f \geq c+g$, $\beta'_{sim} = \dfrac{c+g}{a+e+c+g}$ and

$$\delta\beta_{sim} = \frac{a \times g - c \times e}{(a+e+c+g) \times (a+c)}$$

(4a)

if $b+f \leq c+g$, $\beta'_{sim} = \dfrac{b+f}{a+e+b+f}$ and

$$\delta\beta_{sim} = \frac{(b+f) \times a - c \times (a+e)}{(a+e+b+f) \times (a+c)}$$

(4b)

3. Discrepancies in taxonomic dissimilarity changes according to Jaccard's and beta-sim indices

3.1. General patterns

In Eq. (3) it can be noted that the sign of $\delta\beta_J$ depends on the six parameters describing the historical and current compositions of the two communities (a,b,c,e,f,g), while the sign of $\delta\beta_{sim}$ depends only on 4 or 5 parameters (a,c,e,g if $b+f \geq c+g$, a,b,c,e,f else; Eqs. (4a) and (4b)). To test how this difference can affect the assessment of dissimilarity changes, we computed the Jaccard and beta-sim

indices on the same pool of simulated assemblages. We consider all cases with a,b,c each ranging from 0 to 10 species and e,f,g ranging respectively from −a, −b and −c to 10 that check above conditions (1) and (2).

Considering all the possible cases shows that if the two indices are globally positively correlated (Spearman's rank correlation rho = 0.81, n = 2,939,145, p < 0.001), strong differences are frequent (Fig. 2, and Electronic Appendix Fig. A.1). Indeed, the two indices indicate opposite directions of change, as Jaccard's and beta-sim
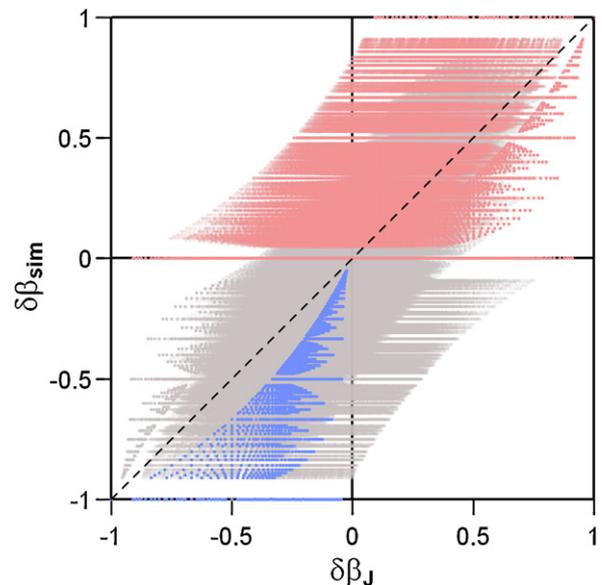

Fig. 2. Relationship between changes in dissimilarity assessed by the Jaccard ($\delta\beta_J$) and beta-sim indices ($\delta\beta_{sim}$). Points represent 2,939,145 simulated hypothetical study cases (see text for details). For the two indices, positive values indicate an increase in the index from historical to current situation. Points in blue show situations with no species historically in common. Points in red show situations with one community historically being a sub-set of the other (i.e. nested communities).

indices have different signs in more than 14% of the simulated pairs of assemblages (four examples of such contradiction are illustrated in Electronic Appendix Fig. A.2). Moreover, in 90% of the cases where the two indices have the same sign they show a relative difference in their values greater than 10%. To go further, below, we discuss two particular situations, although frequent in nature, where Jaccard's and beta-sim indices provide contradictory conclusions about the intensity or even the existence of taxonomic homogenization: communities that historically had no species in common and historically nested communities.

3.2. Particular historical situation: communities had no species in common

This situation is frequent when considering assemblages which have had independent evolutionary trajectories, for example because of strong biogeographic barrier (e.g. isolated islands, different ecoregions). Such a situation is characterized by $a = 0$ and thus following conditions (1) and (2):

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

Historically both indices reached their maximum possible values: $\beta_J = \beta_{sim} = 1$.

Consequently, in such a situation, taxonomic differentiation is impossible. Change in the Jaccard index equals $\delta\beta_J = -e/(e + b + f + c + g)$ and change in the beta-sim index equals: $\delta\beta_{sim} = -e/(e + \min(b+f, c+g))$.

Therefore, as $e \geq 0$ and $0 \leq \min(b+f, c+g) \leq b+f+c+g$, we always have $-1 \leq \delta\beta_{sim} \leq \delta\beta_J \leq 0$. In other words, the magnitude of the homogenization indicated by the beta-sim index is always greater than that indicated with Jaccard's index (blue points in Fig. 2, Electronic Appendix Fig. A.3). For example, for two faunas with identical historical richness of eight species which received the same two non-native species, the drop in the beta-sim index would be of 20% whereas the Jaccard index would only decrease by 11%. More generally, the difference between the two indices is the highest when the respective current numbers of species in the two communities strongly differ (i.e. when $\min(b+f, c+g) << b+f+c+g$).

Note that if $e \neq 0$, $\delta\beta_{sim} = \delta\beta_J \Leftrightarrow \min(b+f, c+g) = \max(b+f, c+g) = 0 \Leftrightarrow \beta'_{sim} = \beta'_J = 0$ and $\delta\beta_J = \delta\beta_{sim} = -1$. In other words the only case where the two indices indicate an identical level of homogenization is when the two communities became totally similar, which may be extremely rare in practice.

Overall, when communities historically had no species in common, the beta-sim index systematically overestimates taxonomic homogenization compared to the Jaccard index.

3.3. Particular historical situation: nested communities

Let us consider the case where in the initial situation, species occurring in community II are a subset of species present in community I. This is the case when comparing fauna from a large ecosystem with fauna from a geographically close smaller ecosystem which only offers a subset of the habitats present in the largest

ecosystem. Such a situation is characterized by $c = 0$ and thus following conditions (1) and (2):

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

Historically both indices reached their minimum possible values: $\beta_J = b/(a + b)$ and $\beta_{sim} = 0$.

The change in the Jaccard index is: $\delta\beta_J = (a \times (f+g) - b \times e)/((a + b + e + f + g) \times (a + b))$, and the change in beta-sim index is: $\delta\beta_{sim} = \min(b+f, g)/((a + e) + \min(b+f, g))$.

As the beta-sim index cannot decrease from its historical null value, $\delta\beta_{sim}$ cannot be negative. In other words, when considering such an historical situation, the beta-sim index will never indicate a taxonomic homogenization (red points in Fig. 2 and Electronic Appendix Fig. A.4).

As an illustration of the insensitivity of the beta-sim index when the two communities are historically nested, consider the particular case where both e and g are also null and f negative (i.e. the species poorest community remains unchanged, no species are introduced but some species present only in the richest community have been extirpated). In this situation, whatever the proportion of species extirpated, the beta-sim index will remain unchanged ($\delta\beta_{sim} = \beta'_{sim} = \beta_{sim} = 0$) while the change in the Jaccard index ($\delta\beta_J = a \times f/((a + b + f) \times (a + b)) = (S_{II}/S_I) \times (f/(S_I + f)) < 0$) depends on the historical species richness ratio and decreases following the increase in the number of species extirpated from the richest community (i.e. decrease of f).

More generally, $\delta\beta_J$ is negative, and thus indicates taxonomic homogenization, when:

$$a \times (f+g) - b \times e < 0 \Leftrightarrow a \times (f+g) < b \times e \Leftrightarrow f+g < \frac{b}{a} \times e$$

As both b and a are by definition strictly positive, in the particular cases where e is also positive, any (f,g) such that $f + g < 0$ (e.g. the number of species extirpated only from the richest community exceeds the number of species introduced only in the poorest community) leads to taxonomic homogenization. In contrast, if e is null and $f + g > 0$, assemblages show taxonomic differentiation.

More importantly, in some situations the Jaccard index decreased while the beta-sim index increased. This contradiction occurs when community II received unique species and is no longer nested in community I while community I loses some of its unique species in a greater proportion than community II receives unique.

The simulated changes illustrated in Fig. 2 and the two particular situations illustrated above showed that the Jaccard and the beta-sim index can indicate opposite direction of changes in taxonomic dissimilarity. Thus these two indices do not estimate the same quantity.

4. Discussion

4.1. Distinction between dissimilarity and turnover

Generally speaking, dissimilarity between two entities based on a given quantity is the proportion (as illustrated by the Venn's diagram in Fig. 1):

$$\text{dissimilarity} = \frac{\text{quantity not shared}}{\text{total quantity}} = 1 - \frac{\text{quantity shared}}{\text{total quantity}}$$

The Jaccard dissimilarity index follows this general definition for the particular case of taxonomic dissimilarity based on species composition, as it equals:

$$\beta_J = \frac{b+c}{a+b+c} = \frac{\text{number of species not shared}}{\text{total number of species}}$$

In contrast, the beta-sim index equals:

$$\beta_{\text{sim}} = \frac{\min(b,c)}{a+\min(b,c)} = \frac{\min(b,c)}{\min(a+b, a+c)}$$

$$= \frac{\text{minimum (number of species not shared)}}{\text{minimum (species richness)}}$$

Thus, the beta-sim index does not measure true dissimilarity. Actually, this is not surprising because the beta-sim index was initially designed to assess turnover in species composition independently of differences in species richness (Lennon et al., 2001), as pointed out by Baselga (2010, in press) and Carvalho et al. (in press).

The confusion about which index to use when assessing taxonomic dissimilarity certainly derived from the issues that have arisen concerning the more general beta-diversity concept. For several years, many indices have been proposed to measure beta-diversity (see Koleff et al., 2003 for a review) and the concept itself is still intensively debated (see Jost, 2007; Tuomisto, 2010a,b; Anderson et al., 2011) 50 years after the seminal work of Whittaker (1960, 1972). Indeed, besides technical debates about which indices
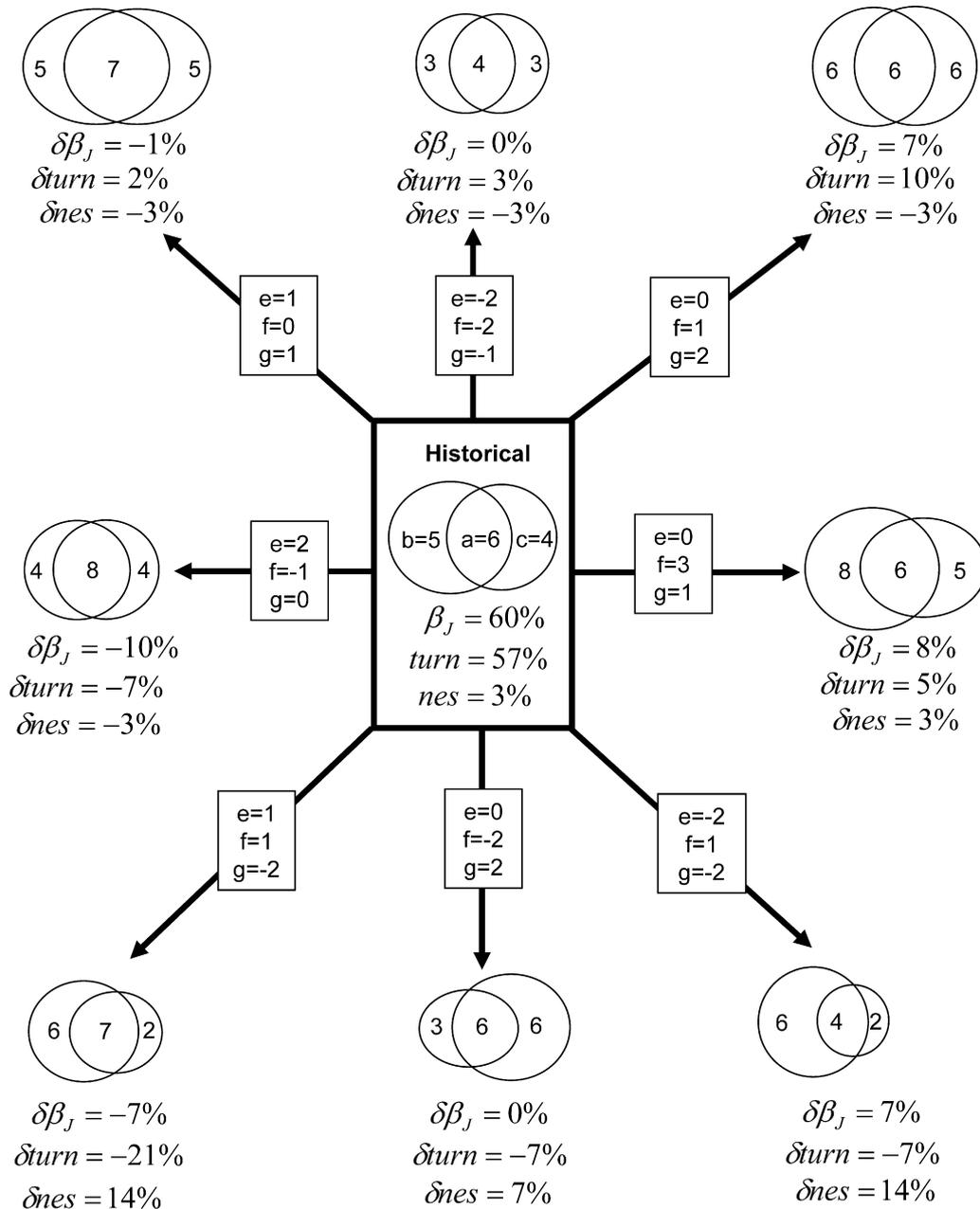

Fig. 3. Decomposition of the changes in dissimilarity ($\delta\beta_J$) into changes of its two components: turnover (δ_{turn}) and nestedness (δ_{nes}). Eight hypothetical study cases illustrate changes from the same historical situation (center) following different levels of introduction and extirpation in the two communities considered (see Fig. 1 for notation). Cases of homogenization (decrease of dissimilarity) are illustrated on the left part while cases of differentiation (increase of dissimilarity) are illustrated on the right part. They can respectively result from congruent changes in turnover and nestedness (middle row) or opposite changes (top and bottom rows). Two examples of how changes in turnover and nestedness of equal intensity but opposite direction can result in unchanged dissimilarity are illustrated above and below the historical situation.

to use (e.g. Jost et al., 2010; Tuomisto, 2010a,b), beta-diversity actually groups several meanings depending on the ecological topic addressed (Anderson et al., 2011). Here, we have only discussed a particular case which is quantifying taxonomic dissimilarity between two communities based on species composition and we revealed that for this purpose the Jaccard index is the only valid.

4.2. Partitioning dissimilarity into turnover and nestedness

Baselga (2010, in press) and Carvalho et al. (in press) emphasized that beta-diversity (*sensu* dissimilarity) can be decomposed into the sum of two independent components:

dissimilarity = turnover + nestedness

Turnover refers to the rate of change in species composition between communities independently from difference in the number of species which is described by the second component. More precisely, Baselga (in press) proposed an explicit additive decomposition of the Jaccard's index:

$$\frac{b+c}{a+b+c} = \frac{2 \times \min(b,c)}{a+2 \times \min(b,c)} + \frac{|b-c|}{a+b+c} \times \frac{a}{a+2 \times \min(b,c)}.$$

$2 \times \min(b,c)/(a+2 \times \min(b,c))$ measures turnover in species composition. It ranges from 0 when the species present in one community are a subset of the species present in the other one (i.e. $\min(b,c)=0$) to 1 when they have no species in common (i.e. $a=0$). This index is close to the beta-sim index even if it compares the minimum number of unique species to the total species richness and not to the species richness of the poorest community (Baselga, in press).

$|b-c|/(a+b+c) \times a/(a+2 \times \min(b,c))$ measures the resultant nestedness component of dissimilarity by accounting for the difference in species richness between the two communities. It equals 0 when the two communities have no species in common (i.e. $a=0$) or the same number of species (i.e. $b=c$) and tends to 1 when the species present in one community are a small subset of the species present in the other one (i.e. $\max(b,c) \gg a > \min(b,c)=0$).

Based on this decomposition, the change in dissimilarity could be decomposed as the sum of the change in species turnover and the change in nestedness. Such a decomposition allows disentangling how the introduction and extirpation processes affect the level of dissimilarity after modifying species richness in each community and/or the number of shared species between communities (Fig. 3). For instance, taxonomic homogenization can result from both a decrease in turnover and a decrease in nestedness if unique species from the richest community are lost while the same non-native species are introduced in the two communities (center left panel of Fig. 3). However, taxonomic homogenization can also result from two kinds of antagonist changes in species turnover and nestedness. First when the increase in species turnover is lower than the decrease in nestedness following introduction of unique species in the poorest community (top left panel of Fig. 3). Second when the increase in nestedness is lower than the decrease in species turnover after extirpation of unique species from the poorest community (bottom left panel of Fig. 3).

5. Conclusion

The mathematical formalism and the corresponding indices presented here are of key interest for assessing the consequences of species introductions and extirpations. Using this formalism, we demonstrate that the Jaccard index is the only one that accurately measures taxonomic dissimilarity while beta-sim index estimate one of its two components, namely turnover. Indeed, the concept of dissimilarity between communities gathers both differences in

their species composition and in their species richness. Therefore, we show the advantage of a decomposition of dissimilarity into turnover and nestedness to disentangle how these two components are driving the changes in dissimilarity after introduction and extirpation of species. We believe that using a relevant and consensual dissimilarity metric, as well as considering its determinants, provides a way to make relevant comparisons across studies dealing with changes in dissimilarities. This is particularly important under the global change context, as there is an increasing need to measure and predict human impact on earth ecosystems. To this aim we provide a R function to compute all the indices presented above (Appendix B).

Further methodological improvements are nevertheless welcome. For instance, Jaccard's dissimilarity index does not allow work with more than two communities. This limitation is generally overcome by averaging all the pairwise changes (Rahel, 2000; Olden and Rooney, 2006). However, it would be easier to develop an index working directly with a pool of N communities, like for example the indices proposed by Baselga (2010, in press). Similarly, one step further would be to consider species relative abundances especially when using local grained data. Indeed, the first signs of abiotic and biotic constraints are often only detectable on species relative abundance (Villeger et al., 2010). For instance, considering only species presence/absence does not allow discrimination between cases where a recently introduced non-native species remains rare and does not modify the abundance of the native species, or on the contrary becomes invasive and dominates the communities but without leading to the local extirpation of native species. With this purpose, the index derived from the Shannon entropy index and the equivalent number of species concept is certainly the most convenient (Jost, 2006, 2007). Ultimately, a unified framework designed to simultaneously measure, with comparable units, the three components of biotic homogenization, including taxonomic, functional and phylogenetic structure, will be of great help in exhaustively describing the effects of human activities on dissimilarity among communities (e.g. Winter et al., 2009; Pool and Olden, in press).

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2012.01.009.

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