A comprehensive formula for decomposing change in community similarity into introduction and extinction events

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Abstract

(Abstract)

The global phenomenon of biotic homogenization is threatening biodiversity worldwide. To explain homogenization, multiple frameworks based on different classifications of introduction and extinction events have been proposed. However, comprehensive and generalized approaches are still lacking. Using mathematical derivation, we present a single comprehensive formula, which demonstrates that similarity changes can be precisely determined by the frequencies of six event types, initial similarity, and total number of species. The formula also shows that the effect directions for all events are type-dependent, while their effect magnitudes generally covary with initial similarity and decrease with increasing species numbers. We argue that future empirical and/or predictive studies of biotic homogenization should pay more attention to these direct factors for a deep understanding of community similarity changes.

Keywords: biotic homogenization, biological invasion, community similarity

Introduction

Biological invasion, climate change, and urbanization are presently altering species compositions worldwide (McKinney and Lockwood 1999, McKinney 2006, Qian and Ricklefs 2006, Magurran et al. 2015, Gossner et al. 2016, Newbold et al. 2018), while changes in community composition are generally associated with higher community similarities and losses of community distinctiveness (McKinney and Lockwood 1999, Olden et al. 2004). The underlying processes of homogenization are still unclear and especially lack theoretical underpinnings (Olden and Poff 2003, Rosenblad and Sax 2017). It was theoretically and empirically proposed that similarity changes are determined by different events (Olden and Poff 2003, Villéger and Brosse 2012, Rosenblad and Sax 2017). For example, the introduction of the same species to two sites would result in an increase in similarity, while the extinction of same native species from two sites would lead to a decrease in similarity. In complement to earlier works on the mathematical description of homogenization (Olden and Poff 2003, Villéger and Brosse 2012), Rosenblad and Sax (2017) provided a concise framework of six types of introduction and extinction events with formula derivations to qualify the relative importance of these events on changes in community similarity. They found that the effects of these events vary according to event type and initial similarity. However, their conclusions mainly derive from simplified assumptions of species richness and number of events, which prevent us from understanding the precise relationships among initial similarity, different event types, and total number of species. Through mathematical derivation (see below) and simulations (Fig. 1), we thus aim to: 1) combine previously identified determinants of change in similarity into a single comprehensive formula; 2) illustrate how these determinants interact with each other; and 3) highlight the important role of gradient in species richness in affecting the magnitude of similarity changes.

With this aim, and as documented by Rosenblad and Sax (2017) and Longman et al. (2018), the types of introductions and extinctions among assemblage pairs can be characterized into seven classes, six of which (I01, I02, I12, E10, E20, and E21) influence change in similarity (Fig. 1). In keeping with Rosenblad and Sax (2017), we use Jaccard's index to quantify community similarity, $J = S / T$, where J is Jaccard's coefficient, S the number of species shared by communities, and T the total number of species in the two communities. We use the subscripts "ini" and "cur" to indicate the metrics for the initial and current assemblage pair, respectively: for example, J_{ini} is the initial similarity, and J_{cur} the current similarity. n_i is the number of species affected by event type i. Based on the definitions of event types, we know that $T_{\mathrm{cur}} = T_{\mathrm{ini}} + n_{\mathrm{I02}} + n_{\mathrm{I01}} - n_{\mathrm{E20}} - n_{\mathrm{E10}}$, and $S_{\mathrm{cur}} = S_{\mathrm{ini}} + n_{\mathrm{I12}} + n_{\mathrm{I02}} - n_{\mathrm{E21}} - n_{\mathrm{E20}}$. Thus, the overall change in similarity is as follows:

$$\Delta J = J_{\mathrm{cur}} - J_{\mathrm{ini}}$$

$$= S_{\mathrm{cur}}/T_{\mathrm{cur}} - J_{\mathrm{ini}}$$

$$= (S_{\mathrm{ini}} + n_{\mathrm{I12}} + n_{\mathrm{I02}} - n_{\mathrm{E21}} - n_{\mathrm{E20}}) / T_{\mathrm{cur}} - J_{\mathrm{ini}}$$

$$= (T_{\mathrm{ini}} \times J_{\mathrm{ini}} + n_{\mathrm{I12}} + n_{\mathrm{I02}} - n_{\mathrm{E21}} - n_{\mathrm{E20}}) / T_{\mathrm{cur}} - J_{\mathrm{ini}}$$

$$= [(T_{\mathrm{ini}} \times J_{\mathrm{ini}} + n_{\mathrm{I12}} + n_{\mathrm{I02}} - n_{\mathrm{E21}} - n_{\mathrm{E20}}) - J_{\mathrm{ini}} \times T_{\mathrm{cur}}] / T_{\mathrm{cur}}$$

$$= [(T_{\mathrm{ini}} \times J_{\mathrm{ini}} + n_{\mathrm{I12}} + n_{\mathrm{I02}} - n_{\mathrm{E21}} - n_{\mathrm{E20}}) - J_{\mathrm{ini}} \times (T_{\mathrm{ini}} + n_{\mathrm{I02}} + n_{\mathrm{I01}} - n_{\mathrm{E20}} - n_{\mathrm{E10}})] / T_{\mathrm{cur}}$$

$$= [n_{\mathrm{I12}} + (1 - J_{\mathrm{ini}}) \times n_{\mathrm{I02}} - J_{\mathrm{ini}} \times n_{\mathrm{I01}} - n_{\mathrm{E21}} - (1 - J_{\mathrm{ini}}) \times n_{\mathrm{E20}} + J_{\mathrm{ini}} \times n_{\mathrm{E10}}] / (T_{\mathrm{ini}} + n_{\mathrm{I02}} + n_{\mathrm{I01}} - n_{\mathrm{E20}} - n_{\mathrm{E10}})$$

Our formula and simulation results rigorously confirm that: 1) more I12, I02, and E10 events tend to lead to homogenization while more I01, E21, and E20 events tend to lead to differentiation (Rosenblad and Sax 2017) (Fig. 1); and 2) for I02 and E20, the effect magnitude of similarity negatively covaries with initial similarity, while the effect magnitudes of I01 and E10 positively covary with initial similarity. Importantly, our results also reveal the crucial role of the total number of species in determining the magnitude of similarity changes (Olden and Poff 2003) (Fig. 1). Namely, the magnitude of change in similarity for all six events decrease with the increasing number of initial species. We further demonstrate that the effects of I12 and E21 are mediated by the initial similarity when Sørensen's index of similarity is adopted (Supplementary material Appendix 1). Because the number of species that are initially shared or unique to different sites influences the potential number of extinctions, some extinction or introduction events (e.g. E10, E20, E21, I12) are ecologically constrained by initial similarity and total species richness (Fig. 1).

Using the formula, we demonstrate that the direction and magnitude of change in community similarity are determined by the frequencies of six introduction and extinction event types, initial similarity, and total species richness. The formula provides a unified theoretical framework for understanding homogenization and differentiation processes, which are documented in numerous empirical studies (Qian and Ricklefs 2006, Villéger et al. 2011, Toussaint et al. 2014, Magurran et al. 2015). We also provide an interactive web application for visualizing the simultaneous effects of different factors on similarity changes (<https://similarity-changes.shinyapps.io/sim_app/>). Our formula could potentially be used to predict future patterns of similarity changes based on current community compositions and the estimated introduction and extinction rates under future global change (Olden and Poff 2003, Rosenblad and Sax 2017, Longman et al. 2018). The formula could also provide a useful framework in which to explore how other factors (such as spatial variation in human activities) determine the frequencies of different event types, which in turn drive patterns of change in similarity. Our work comprehensively and rigorously combines previously identified determinants of change in similarity such as different event types and initial similarity. Further, our results emphasize that total richness should be considered when predicting or explaining the magnitude of change in similarity among assemblage pairs.

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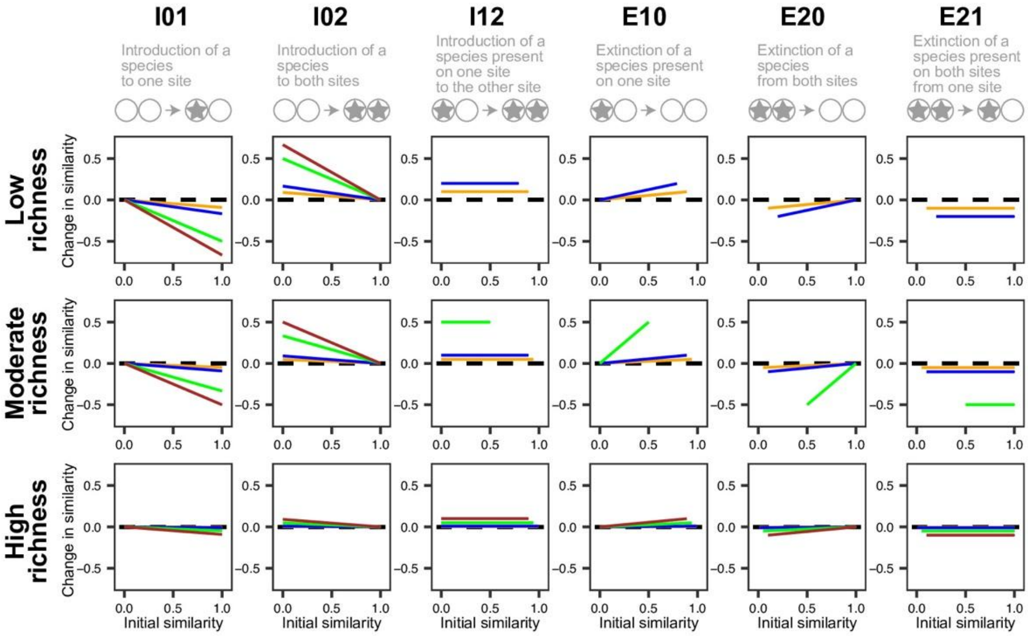

Figure 1. Relationship between initial similarity and change in similarity for each event type under different initial richness scenarios based on the Jaccard-derived formula. The top diagrams illustrating the events are adopted from Longman et al. (2018); circles indicate communities, and stars the introduced or extinct species. Low, moderate, and high richness were set at 50, 100, and 1000, respectively. For a given event type, four instances (orange line for 5 events, blue for 10, green for 50, and brown for 100) were used to demonstrate the effects of event frequency on the relationship, with the numbers of other event types kept as zero.