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FORUM

Improving approaches to the analysis of functional and taxonomic biotic homogenization: beyond mean specialization

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Summary

1. Abadie *et al., Journal of Ecology*, 99, 2011, 1134 claim that 'landscape disturbance causes small-scale functional homogenization but limited taxonomic homogenization'. This statement does not seem to accurately summarize their results.

2. Abadie *et al.* provide no strong arguments in favour of a cause and effect relationship between landscape disturbance and functional homogenization because their approach is correlational.

3. Abadie *et al.* associate an index of mean community specialization with functional biotic homogenization (BH), and they in turn associate functional BH with ecosystem functioning. However, the community specialization index is associated with a very specific kind of 'function' – the species response – which has no clear link with ecosystem functioning. This problem is frequent in the literature on biotic homogenization.

4. There is no clear sign in the data shown by Abadie *et al.* that metrics incorporating species attributes are 'much more reliable' than taxonomic diversity indices.

5. As frequently observed in the literature on biotic homogenization within communities, their results show no sign of loser or winner species or of 'extirpation of specialist species'. Therefore, there seems to be no evidence in support of the biotic homogenization model they propose.

6. *Synthesis.* The Average Community Specialization – a mean specialization index– is in itself incapable of identifying loser and winner species and has no clear link with ecosystem functioning. Methods other than mean trait approaches should be used to study either functional homogenization or the extirpation of specialist species.

Key-words: determinants of plant community diversity and structure, habitat fragmentation, habitat specialization, conservation biology, biodiversity, biometry, statistics, response trait, effect trait, functional homogenization

Introduction

Biotic homogenization (BH) is a biodiversity dynamics model that can be described as a temporal increase in community similarity (McKinney & Lockwood 1999). Abadie *et al.* (2011) studied the biotic homogenization of plant communities in space by relating diversity indices and a specialization index with landscape fragmentation or landscape conversion. They based their approach on an interesting distinction between functional biotic homogenization and taxonomic homogenization. They claim that 'landscape disturbance causes small-scale functional homogenization but limited taxonomic homogenization', 'via the extirpation of specialist species'. They also assert that 'metrics incorporating species sensitivity to disturbance (such as species specialization to habitat) appear much more reliable than taxonomic diversity for documenting the response of communities to disturbance' (all passages either from the Title or the Summary of Abadie *et al.* 2011). Although I agree that these are interesting lines of investigation, the authors' results do not support their conclusions. I explain my reasoning herein. In particular, I insist on the limitations of BH approaches, such as the Average Community Specialization (ACS), which are based solely on a mean trait approach. I argue that decreases in ACS alone cannot distinguish situations where specialized species are losing and generalist species are winning from some other situations resulting in changes of community composition.

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INADEQUATE REFERENCE TO CAUSATION

My first remark is obvious, so obvious that I am surprised to be making it here. Both in the title and in the summary, the authors refer to a cause–effect relationship between landscape disturbance and functional homogenization, even though their approach is based solely on correlations between biodiversity data and landscape data. Furthermore, they insufficiently consider confounding factors in their design and analysis. Has the authors' concern for communication overruled their scientific rigour? There is general agreement in ecology – as in other sciences – that correlation does not equate with causation. The classical view is that proof of causation is best served by the use of experimental set-ups, which are quite different from observational studies. Some authors are open to accepting other sources of evidence – including observational data – to indicate causation (Hill 1965; Holland 1986; Pickett, Kolasa & Jones 2007); but even in this more open perspective, a cause–effect relationship cannot be proven from a correlation based on a *single* source of evidence, especially when no particular care is taken to investigate the features that could lead to misinterpreting the simple correlation as being causal (identified by Hill 1965).

BIASED CONSIDERATION OF FUNCTIONAL AND TAXONOMIC HOMOGENIZATION

The title and summary of Abadie *et al.*'s article not only state that landscape disturbance causes functional BH, but also state that there is limited taxonomic homogenization concurrent to this functional homogenization. The authors conclude that 'metrics incorporating species sensitivity to disturbance […] appear much more reliable than taxonomic diversity for documenting the response of communities to disturbance' (in the Summary). However, the analysis of the results proposed by Abadie *et al.* (2011) to document these statements is biased and unbalanced.

The authors do establish a link between landscape variables and *functional* BH thanks to five statistically significant relationships out of the eight explicitly tested in the article, which correspond to interactions between the four habitat types and the two landscape variables. However, they then go on to justify the so-called 'limited' relationship between landscape variables and *taxonomic* BH based on the weaker relationships they found (compared with previous studies on taxonomic BH in plants) between their two landscape variables and beta-diversity. What the authors mean by a 'weak' relationship between landscape variables and beta-diversity is not clear – is it weak in terms of statistical significance or weak in terms of the magnitude of the effects? The first interpretation seems to be the one supported by the authors because the summaries of the statistical significance tests described by Abadie *et al.* (2011) do not include information on the estimates of the effects, contrary to what, for example, Yoccoz (1991) advises.

If we now compare the statistical significance of the relationships between landscape variables and either functional BH or within-habitat β-diversity, which is the version of taxonomic BH that is the closest to the way functional BH is analysed (cf. Following), we find only one statistically significant relationship out of two for taxonomic BH (see Abadie *et al.*'s Figure 3), compared with five of eight for functional BH. In this case, can we conclude that 'metrics incorporating species sensitivity to disturbance […] appear much more reliable than taxonomic diversity for documenting the response of communities to disturbance'? In other words, Is the percentage of statistically significant relationships a measure of the reliability of the method? If so, then why not conclude that taxonomic diversity – four of four significant relationships based on α and γ diversity (cf. Figure 2) – is more reliable than either taxonomic or functional BH to document the community response to disturbance?

Finally, the authors downscale the degree of influence that landscape variables have on *taxonomic* BH by using a method different from the one they use for *functional* BH. Indeed, when modelling the relationship between landscape variables and functional BH, the authors model the effect of the individual habitat type as well as the interactions between habitat types and landscape variables. In contrast, in the case of taxonomic BH, the effect of individual habitat types as well as potential interactions between habitat types and landscape variables are not taken into account – which would have been possible for α and within-habitat β-diversity.

LOOSE DEFINITIONS AND UNCLEAR LINKS BETWEEN CONCEPTS: 'FUNCTION', HABITAT SPECIALIZATION AND SENSITIVITY TO DISTURBANCE, HABITAT FRAGMENTATION

Abadie *et al.* (2011) seem to include species specialization to habitat in the functional characteristics of the species, 'with possible consequences for ecosystem functioning' (p. 1134). In doing so, the authors link species specialization with the functional role of species in ecosystems. This appears irrelevant to me: as defined by Abadie *et al.* (2011), specialization is a description of the species' response to habitat and is a very specific kind of function – related to functional response groups which are defined based on the response of species to environmental factors (Jax 2005; Lavorel & Garnier 2002). It seems that the authors have confounded functional *response* groups with functional *effect* groups, that is, functional groups of species that are defined according to the effects species have on the environment and ecosystem functioning (Lavorel & Garnier 2002; Naeem & Wright 2003; Jax 2005). Therefore, Abadie *et al.*'s use of the term 'functional' is misleading, especially when the authors evoke possible consequences on 'ecosystem functioning'. This confusion seems to be rather common in the literature on functional homogenization (Table 1): approximately one of three articles quotes a potential link between functional homogenization and ecosystem functioning, although none of the articles clearly distinguish between *response* and *effect* ecological traits. Furthermore, most of the articles either used response traits related mostly to habitat gradients and not to ecosystem functioning, or

Table 1. Review of the species traits considered by published papers that cited the keyword 'functional homogenization' in the Scopus® data base, on the following issues: Are response and effect traits distinguished explicitly? (column 2); Is functional homogenization based on response traits, effect traits or other traits (e.g. physiological or life-history traits not clearly related to ecosystem functioning)? (columns 3–5); Is there a reference to a link between functional homogenization and ecosystem functioning? (last column)

Reference	Distinguishes between response and effect functional traits/groups	Uses Response functional trait/groups	Uses Effect functional trait/groups	Uses species traits not clearly or directionnally linked to ecosystem functioning	Refers to a link between functional homogenization and ecosystem functioning
Holway & Suarez (2006)	No	No	No	Yes	No
Julliard *et al.* (2006)	No	Yes (response to habitat type)	No	No	Yes (community level, not ecosystem level)
Olden (2006)	No	Yes (response to disturbance)	Yes (notion of roles)	Not clear	Yes (but critical)
Olden & Rooney (2006)	No	No	No	Yes	No
Devictor *et al.* (2007)	No	Yes (response to habitat type)	No	No	No
Croci, Butet & Clergeau (2008)	No	Yes (response to habitat type)	No	Yes	No
Devictor *et al.* (2008b)	No	Yes (response to habitat type)	No	No	No
Winter *et al.* (2008)	No	No	Yes (notion of roles)	Yes	Yes
Janion, Worland & Chown (2009)	No	No	No	Yes	No
Ortega-Álvarez & MacGregor-Fors (2009)	No	No	No	Yes	No
Bellisario, Cerfolli & Nascetti (2010)	No	No	No	No	No
Clavero & Brotons (2010)	No	Yes (response to habitat type)	No	No	Not clearly
Van Turnhout *et al.* (2010)	No	No	No	Yes	No
Verberk *et al.* (2010)	No	No	No	Yes	Yes
Baiser & Lockwood (2011)	No	No	No	Yes	Yes
Barnagaud *et al.* (2011)	No	Yes (response to habitat type)	No	No	No
Clavel, Julliard & Devictor (2011)	Not clearly	Yes (response to habitat type)	No	No	Yes
Clavero & Hermoso (2011)	No	Yes (response to habitat type)	No	Yes (invasive/native; body size)	No
Lizée *et al.* (2011)	No	No	No	Yes	Yes
Gascón *et al.* (2012)	No	Not clear	Not clear	Not clear	Yes
Tobias & Monika (2012)	No	No	No	Yes	Yes
Pool & Olden (2012)	No	No	No	Yes	Yes
Vitule, Skóra & Abilhoa (2012)	No	No	No	Yes	No

We did not consider that the study of trophic traits belonged to effect traits – that is, traits that summarize the effect of species on ecosystem functioning: classification in the fourth column (effect traits) was therefore more stringent than that in the third column. The article by Lende (2010) could not be analysed because it was written in Spanish.

involved quantification of functional homogenization based on traits other than response or effect traits. Very few articles actually included true effect traits.

Another part of the literature studies the relationship between response and effect ecological groups or traits. We retrieved this bibliography with the keyword search: ('functional' AND (('response trait' AND 'effect trait') OR ('response group' AND 'effect group'))) under Scopus®. It seems that two schools of thought coexist here. On the one hand, some argue that there is no direct link between 'functional response groups' and 'functional effect groups'(Jax 2005) and that the two concepts should be clearly separated in any analysis (Suding *et al.* 2008). On the other hand, some studies found a relationship between the two types of traits

(Gross *et al.* 2008 and Pakeman 2011); however, none of them included response traits to land-use or habitat type. Some other studies obtained mixed results, depending on the scale of analysis (Blanco *et al.* 2007).

It was my surprise when writing this article to discover the almost complete independence of the two fields in the literature – functional homogenization on the one hand, and functional response and effect traits on the other: no reference was found in Scopus® that cited both groups of keywords I used to gather papers in these two fields of the literature. I therefore fully agree with Luck *et al.* (2012) that animal ecologists working on ecological traits – and I dare add on functional homogenization – 'need to develop more coherent and systematic trait-based approaches that are broadly applicable…/… drawing specifically on the substantial progress made in this area for plants'. Indeed, although some authors believe that animal trait analysis is by nature more remote to ecosystem functioning than plant trait analysis (e.g. Pool & Olden 2012) and some others suppose that specialist species– in terms of habitat selection – should also bear special functions in ecosystems (Clavel, Julliard & Devictor 2011), a more careful and rigorous selection of traits, in view of their link with ecosystem functioning, is an interesting line of research.

Secondly, Abadie *et al.* (2011) also include species specialization to habitat in species sensitivity to disturbance (p. 1134). This does not seem clear to me: some specialized species could be favoured by disturbance (e.g. early successional species), while other specialized species would be negatively impacted by disturbance (e.g. forest species or late-successional species; cf. Clavero, Brotons & Herrando 2011 and references cited therein for such examples).

Thirdly, it would have been interesting to adopt a more pluralistic view of habitat fragmentation rather than focusing only on edge density (as e.g. Zipkin, Dewan & Andrew Royle 2009 did) and to analyse habitat quantity along with habitat fragmentation (as suggested e.g. by Fahrig 2003): there is much more to habitat fragmentation than mere edge density and there is much more to habitat limitation issues than mere habitat fragmentation.

INADEQUATE QUANTIFICATION OF FUNCTIONAL HOMOGENIZATION

My fourth problem with Abadie *et al.* (2011)'s approach is related to the way they quantify functional homogenization. Indeed, the index they use is not associated with the notion of similarity as in the original definition of homogenization; instead, they use Average Community Specialization (ACS; similar to the Community Specialization Index developed by Devictor *et al.* 2008a). The ACS of a given community is the mean value of the 'specialization index' of all the species in that community; ACS therefore belongs to the family of mean trait approaches. Incidentally, it is interesting to note that the specialization index used by Abadie *et al.* (2011) has an odd property: the minimum of its mean value over species – under 100 as shown in Figure 5 – is less than the minimum value over all the species indicated in the text (262.9, p. 1137).

However, the increase in functional or taxonomic similarity between plots – which defines biotic homogenization – can accompany increases as well as decreases in the mean specialization of the communities. For example, in the case studied by Abadie *et al.* (2011), a strong increase in forested area in the study region would probably have resulted in both biotic homogenization (through an increase in the similarity of communities due to the homogenization of habitat types) and an increase in mean specialization (through an habitat type effect– cf. Figure 4, and through a decrease in habitat fragmentation – cf. Figure 5).

This problem is not confined to Abadie *et al.* (2011)'s article (see Table 2): while around half of the papers quantify functional homogenization *within communities*, with tools

Table 2. Review of the quantification of functional homogenization in published articles that cited the keyword 'functional homogenization' in Scopus® data base, along the following lines: – Is functional homogenization defined within communities or between communities (column 2)? What are the metrics or methods used to quantify homogenization (column 3)? I have here only retained the references in Table 1 that actually quantified functional homogenization

Reference	Within or between communities?	Kind of metrics used
Holway & Suarez (2006)	Within	Mean trait & trait diversity
Julliard *et al.* (2006)	Within	Mean trait
Olden (2006)	Between	Similarity indices
Olden & Rooney (2006)	Between and within	Jaccard similarity index; discusses other methods
Devictor *et al.* (2007)	Within	Proportion of generalist species
Devictor *et al.* (2008b)	Within	Mean trait
Winter *et al.* (2008)	Between	Morisita-Horn similarity
Janion, Worland & Chown (2009)	Within	Histogram of trait
Clavero & Brotons (2010)	Within	Mean trait
Verberk *et al.* (2010)	Between and within	Bray–Curtis similarity, abundance of LHStrategies groups
Baiser & Lockwood (2011)	Between	Bray–Curtis similarity
Barnagaud *et al.* (2011)	Within	Mean trait
Clavel, Julliard & Devictor (2011)	Within	Mean trait
Lizée *et al.* (2011)	Between	CCA & ANOSIM
Pool & Olden (2012)	Between	Bray–Curtis similarity and beta-diversity
Tobias & Monika (2012)	Between	Beta-diversity based on Rao Q
Vitule, Skóra & Abilhoa (2012)	Between	Jacard and Bray–Curtis similarity, beta-diversity

ANOSIM, Analysis of Similarities; CCA, Canonical Correspondence Analysis.

such as the calculation of a mean trait – for example, a specialization index – over species in the community, the other half considered tools that quantified similarity *between communities*, being closer in this respect to the original definition of biotic homogenization. Authors disagree on whether functional homogenization can be studied *within* communities: Tobias & Monika (2012) for example, regret that the within community scale be used without further qualification as an approach to functional homogenization: 'Several studies addressing functional homogenization have not used the term as originally defined, that is, a decrease in the functional dissimilarity between species assemblages (Olden & Rooney 2006), but have instead used it to describe a loss of functional diversity within species assemblages, that is, a decrease in the functional dissimilarity among coexisting species (e.g. Devictor *et al.* 2008a,b; Winter *et al.* 2008)'. This quotation is, however, in contrast with the very method used by Winter *et al.* (2008) – who quantify function homogenization between communities; cf. Table 2. This quotation is also in contrast with the quoted article by Olden & Rooney (2006), because these authors admit the possibility of studying biotic or functional homogenization within communities– for example, by using diversity, evenness or measures of functional diversity (Petchey & Gaston 2006).

The central question might not be whether we can study functional homogenization within communities as well as between communities. I think we can do both, much like we can study diversity at the so-called alpha, beta and gamma levels. The question is more how we should quantify functional diversity within communities. Indeed, the majority of the articles studying functional homogenization within communities used mean trait approaches, often based on species traits associated with species specialization to habitat, much like the ACS used by Abadie *et al.* (2011). The only article I found that justifies this choice (Devictor *et al.* 2007) seems to replace the notion of diversity – to quantify within-habitat homogenization – or similarity – to quantify between habitat homogenization – with a model of replacement of specialist species by generalist species. I wonder whether a different term should not have been used for this different notion, thus favouring a side by side analysis of functional homogenization and of the replacement of specialists by generalists, rather than a substitution of one approach by the other.

NO SIGN OF SPECIALIST EXTIRPATION AND BIODIVERSITY LOSS

We have seen that ACS is not directly related to biotic homogenization (BH). We will here study why it is also not directly related to biotic impoverishment, even for the specialist part of the communities. I therefore disagree with the statement that 'community specialization can thus be seen as an effective indicator (Balmford *et al.* 2003), accounting for the widespread replacement of specialist species ('losers') by more tolerant generalist species ('winners')' (p. 1141). I also disagree when the authors speak of the 'extirpation of specialist species' (Summary). Indeed, overall fitness or abundance of both specialist and generalist species can either decrease or increase when ACS increases. For example, suppose the specialized species in a given region increase in abundance by 10%, while generalists increase by 50%. An ACS-based analysis of this change would conclude that biotic homogenization had occurred. This is because the index depends on relative abundance, not on absolute abundance. This example shows that a decrease in the ACS only allows us to conclude that specialist species are *relative* losers compared with generalist species. It does not allow us to say that these specialists are 'loser' species if by that we mean they have effectively declined in abundance or fitness. Diversity indices have also been shown to have this property (Gosselin & Gosselin 2004).

THE NEED FOR FURTHER METRICS TO DOCUMENT SPECIALIST EXTIRPATION

Abadie *et al.*'s (2011) results showing an ACS decline parallel to landscape fragmentation are contradicted by the absence of statistically significant relationships between the specialization index of the commonest species and their response to landscape disturbance: a decrease in specialist species *relative to* generalist species concomitant with landscape disturbance should have been accompanied by a decline in the ACS and by a statistically significant negative relationship between the degree of specialization and the species' response to landscape disturbance. The authors distrust their multispecies result because they suppose a different statistical power between their species response analysis and their ACS analysis. However, they base their distrust solely on differences in degrees of freedom: around 50 for the species response analysis versus 350 for the ACS analysis. Here too I disagree with the authors' interpretation: the ACS analysis is based on a linear mixed model in which landscape fragmentation is a variable that is constant within each random effect corresponding to the survey squares. In other words, landscape variables are 'outer' variables (in the words of Pinheiro & Bates 2000): the degree of freedom associated with the estimate of landscape effects is around 50 – the order of magnitude of the number of survey squares –, not 350. Furthermore, I do not understand why the ACS was analysed at the plot scale while all the other analyses seem to have been done at the survey square scale.

In the absence of further information, I retain both pieces of evidence put forward by Abadie *et al.* (2011): (i) there is a decline in ACS with landscape fragmentation and (ii) for the commonest species, there is no correlation between species specialization and the species response to landscape fragmentation. These results can be explained in different ways: the ACS trend may have mainly been influenced by the rarest species; the species response model may be inadequate (it is a linear model for species abundance data which are non-negative data with potentially a large number of zeros); or the two analyses may have different levels of statistical accuracy and power.

To sum up, in addition to my remarks on causation and a biased consideration of taxonomic and functional homogenization, the main point is that mean trait approaches such as

the ACS need to be complemented by other metrics if we wish to interpret BH in terms of extirpation of specialist species or in terms of functional homogenization impacting ecosystem functioning, as Abadie *et al.* did. To document the extirpation of specialist species, the analysis of species-level data carried out by Abadie *et al.* (2011) is an interesting option but requires more adequate statistical tools (e.g. Gelfand *et al.* 2005; Zipkin, Dewan & Andrew Royle 2009). One option would be to define ecological groups, based on the value of specialization, and to study the response of the species richness and the *absolute* abundance of these groups to landscape characteristics (as in e.g. Barbier *et al.* 2009). I insist that absolute abundance should be used – not relative abundance as in, for example, Filippi-Codaccioni *et al.* (2010) – because absolute abundance seems to be a more robust way to document species extirpation than relative abundance. Species-level and ecological-group level analyses are complementary: the latter allow us to take the rarest species into account while the former provide a less dichotomous assessment of species traits – but see Zipkin, Dewan & Andrew Royle (2009).

The dichotomy proposed by Abadie *et al.* (2011) between functional homogenization and taxonomic homogenization or diversity is not the most appropriate. Instead, we should distinguish the study of functional homogenization from that of specialization; there is indeed a tendency to equate both aspects and to restrict functional homogenization to mean specialization (cf. Table 2), for no clear reason. It might help to reconnect the research communities working on functional traits and those working on functional homogenization. These two lines of research should in turn be distinguished from an area closer to conservation biology: studying the extirpation of specialist species. Here too, analyses should not be based solely on mean specialization but should include the relationship between the level of specialization and the response to environmental gradients of either species-level absolute abundance or frequency, or ecological-group level species richness or abundance. Mean trait approaches alone are insufficient, whether it be in functional ecology or in conservation biology.

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