The community ecology of invasive species: where are we and what's next?

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Alien species are continually introduced in most regions of the world, but not all survive and coexist with the resident native species. Approaches analyzing the functional (or phylogenetic) similarity between invasive species and native communities are increasingly employed to infer the processes underlying successful invasions and to predict future invaders. The relatively simple conceptual foundations have made these approaches very appealing and therefore widely used, often leading to confusion and hampering generalizations. We undertook a comprehensive review and synthesis of the functional similarity approach in invasion community ecology to clarify its advantages and limitations, to summarize what has been learned thus far, and to suggest avenues for future improvement. We first present the methodological state of the art and provide general guidelines. Second, by organizing the published literature around seven key questions in invasion ecology we found cumulative evidence that: at large spatial scales phylogenetic relatedness of invasive and native species is a good predictor of invasion success, but a poor predictor of invasion impacts; at fine spatial scales, community resistance to invasion tends to increase with native species diversity and with similarity to the invaders, consistent with patterns emerging from biotic interactions. In general, the processes filtering invaders appear to vary across species' invasion stage and along environmental gradients. Nonetheless, we found conflicting evidence for differences in community assembly processes between invasive and native species, and between the invader's native and adventive ranges. Finally, we propose four important avenues for overcoming some of the identified methodological and conceptual limitations of the approach, in particular by integrating observational and experimental analyses and by explicitly considering species' demographic rates and complex biotic interactions. Although the functional similarity approach bears intrinsic limitations, it still offers many opportunities in invasion community ecology at large spatial scales.

The introduction of new species through human intervention is exponentially increasing worldwide, often with dramatic impacts on native biodiversity and ecosystem functions (Sax and Gaines 2008). Understanding the mechanisms by which introduced species establish and become invasive and finding strategies to anticipate new invasions is a key step for mitigating their impacts. Three main assembly processes (or filters, according to the community ecology filtering metaphor, Keddy 1992) are thought to influence the success of introduced species outside their native range: 1) environmental, 2) biotic and 3) dispersal filtering (Theoharides and Dukes 2007, Richardson and Pyšek 2012). First, local environmental conditions of the new range filter species from the pool of introduced species based on their ecological niches and physiological adaptations (environmental filtering). Second, competition from the resident species selects among the environmentally adapted aliens those that can coexist within local communities through exploitation of unused resources or replacement of competitively inferior native species (biotic filtering or biotic resistance). Finally, natural or human mediated dispersal determines which species spread into natural communities across the landscape (dispersal filtering). Ultimately the interplay of these three simple processes determines which species become invasive and which communities are invaded over large biogeographical scales (Richardson and Pyšek 2012).

While there is broad consensus on the importance of these processes in structuring invasion patterns, studying them at the large spatial scales relevant for invasion management and prevention has proven extremely challenging. Small-scale competition experiments typically lack generality to make regional predictions and extrapolations, while data limitations have hindered our understanding and accurate prediction of invasions at large scales. Recently, the availability of large community datasets combined with functional information on species ecological strategies has opened new avenues for overcoming these challenges. Ecological similarities (or niche overlaps) among species within communities can now be estimated based on functional traits or on phylogenetic relationships (under the assumption that closely

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related species share similar traits; Webb et al. 2002, Letten and Cornwell 2015). This new functional similarity framework supports inferences regarding the likelihood and the outcome of alternative community assembly processes via the analysis of these ecological similarities (Diamond 1975, Keddy 1992, Webb et al. 2002). This approach fosters a process-based understanding of invasions and potentially enables predictions at large spatial scales (Darwin 1859).

The functional similarity approach is based on the premise that the different assembly processes will leave detectable signatures in functional and phylogenetic similarity patterns of co-occurring native species and invaders. If, as postulated by neutral theory (Hubbell 2001), species co-occurrence is mostly structured by dispersal (immigration) and stochastic forces (such as demographic stochasticity and local extinctions), species niches should play no role and functional similarities should be randomly distributed. On the contrary, niche theory predicts that species functional traits should influence species co-occurrence because of environmental filtering and biotic interactions. Environmental filtering should lead to the co-occurrence of species with similar adaptations to the local environmental conditions, while biotic filtering should limit this similarity because the more species overlap in their niches the higher is the chance of competitive exclusion of one species (Weiher and Keddy 1999, Chesson 2000). In invasion ecology, the contrast of these two expectations in niche theory is widely known as Darwin's naturalization conundrum (Darwin 1859, reviewed in Rejmánek 1996, Procheş et al. 2008, Thuiller et al. 2010). However, a species can survive biotic filtering either by being sufficiently dissimilar in resource use from the resident species (benefiting from resource opportunities), or by possessing superior competitive ability and excluding weaker competitors (MacDougall et al. 2009, Mayfield and Levine 2010, Li et al. 2015a). Following this reasoning, under strong biotic filtering dissimilar species can coexist if several resources limit coexistence, while only the best competitors should survive if coexistence is limited by one main resource (i.e. those sharing similar highly competitive traits

for that resource, Mayfield and Levine 2010, Gallien et al. 2015). According to these simple assumptions, by studying patterns of similarity among coexisting species (or functional diversity) and their deviations from randomness or from neutrality it is possible to infer the past processes that have driven community assembly and invasion and to predict new invasions.

The framework relies only on the calculation of an index summarizing species (dis)similarity and on a statistical test to evaluate deviations from null expectations. However, in the simplicity of this approach lie also its limitations. Deducing patterns from processes is always a risky business in ecology, among other things because many assumptions have to be made, because different processes may result in similar patterns and because processes acting in concert may result in blurred patterns. Nevertheless, it is widely accepted that, if duly validated and correctly applied, this functional approach represents our best hope of significantly improving our understanding of invasions at large spatial scales (Procheş et al. 2008).

Accordingly, the functional (or phylogenetic) similarity approach has been increasingly applied in the context of invasion community ecology to gain insights into many long-standing questions (Procheş et al. 2008, Thuiller et al. 2010; Fig. 1 and 2). In its most classical application, similarity of alien species to native species in a community has been used to predict 1) which species will become invasive and 2) which native communities will prove resistant to invasion. A large body of literature has then focused on understanding 3) which processes drive coexistence between invasive and native species. More recently a number of further open questions in invasion ecology are starting to be addressed with this approach, including whether and how processes involved in invasion success 4) change with species invasion stage, and 5) vary along environmental gradients (Richardson and Pyšek 2012), 6) whether invasive species coexist with the natives via the same processes that rule native species coexistence (Kempel et al. 2013, Ordonez 2014) and 7) whether different processes limit invasive species in their introduced
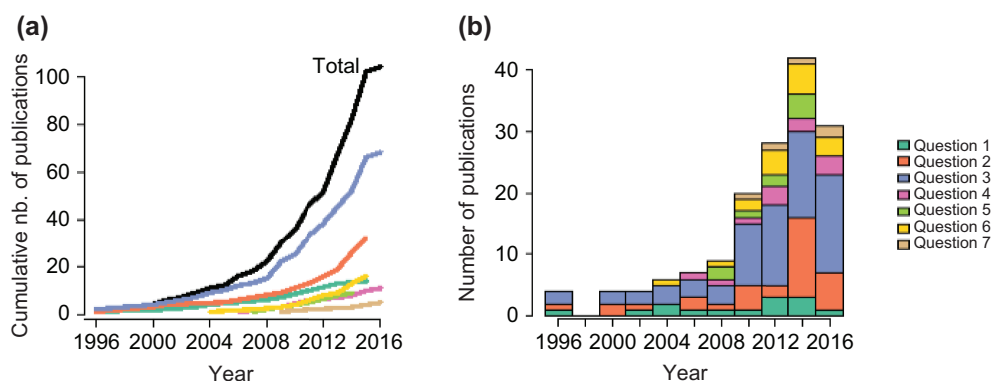

Figure 1. Relative interest in community assembly processes and invasion over the past 20 yr, as estimated from the number of articles published in peer-reviewed journals. (a) The total cumulative number of studies published is shown in black, and colour lines represent the different questions addressed in these articles (see Fig. 3 for the list of the 7 questions considered). (b) Frequency of studies published over the years (per biennials) divided by the seven questions. The articles were identified from systematic search in ISI with the search rule: (Darwin's naturalization OR assembly rule* OR community assembly) AND (functional OR trait OR phylogen*) AND (similar* OR distance* OR differences OR relatedness) AND (invasive OR alien OR exotic OR native OR naturaliz*), accessed on January 2016. All articles were verified to match the topic of interest, and their list was completed with citations therein. The full list of articles is presented in Supplementary material Appendix 1.
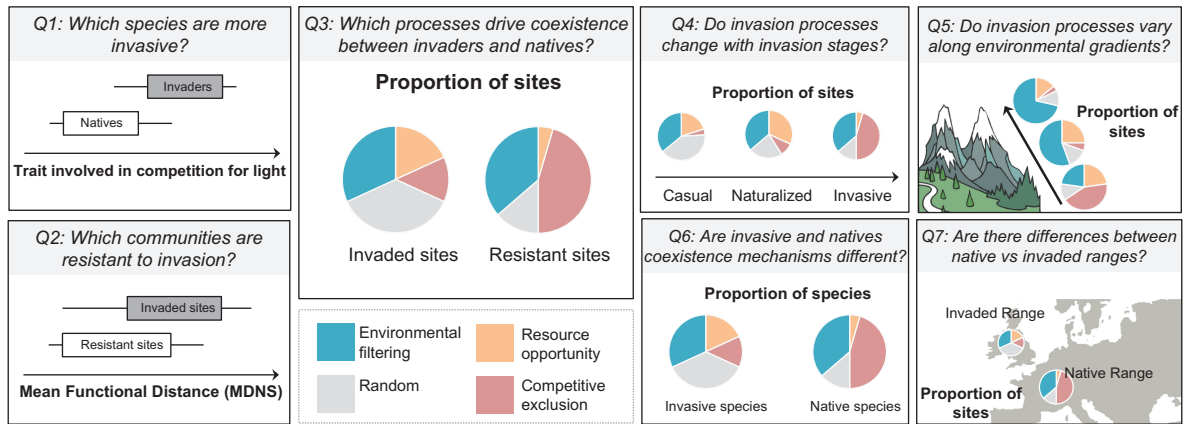
Figure 2. Illustration of the 7 key questions relative to the mechanisms of invasion that can be tackled with community ecology approaches.

vs native range (Colautti et al. 2004, Hierro et al. 2005, Blumenthal 2006). This proliferation of studies has brought many insights, but has also lead to the multiplication of the available metrics and statistical tools, making it difficult to assess, also given the intrinsic limitations of the approach, the progress of the field towards finding answers.

We reviewed and synthesized the growing body of literature adopting a functional similarity approach in invasion community ecology, with the goal of identifying the most promising ways forward for this growing discipline. First, we present the methodological state of the art by synthesizing the different tools and offering some practical guidelines. Second, we organize the relevant published literature along the seven broad questions identified above in order to assess what we have learned so far (Fig. 2). We highlight the questions that have already received much attention and those that require more attention. Finally, by drawing on the critical synthesis from the two previous sections we identify gaps in our current knowledge and outline perspectives for future work that can foster our mechanistic understanding and prediction of biological invasions. We conclude that the functional similarity approach has not yet allowed to draw many definitive conclusions leaving still many open questions, but that by applying it correctly and complementing it through new advances in ecological research it still offers many opportunities in invasion community ecology at large spatial scales.

Methodological state of the art

When using species similarity patterns to predict successful invasions and infer coexistence mechanisms it is necessary to combine similarity indices and statistical tests. A wide variety of such indices (Cadotte et al. 2010, Schaefer et al. 2011, Maitner et al. 2012) and tests (Strauss et al. 2006, Diez et al. 2008, Carboni et al. 2013) have been applied in the invasion context. However, this diversity often makes it difficult to identify the best methodology to employ e.g. for identifying the process under investigation. Here, by systematically reviewing the available tools, we aim at clarifying their underlying assumptions and limitations, and providing guidelines for correct application (Box 1).

Species-based and community-based indices

We compare two main types of indices that are useful in invasion community ecology: species-based vs community-based indices. Species-based indices quantify the dissimilarity between one focal species (i.e. the invader) and the rest of the community, while community-based indices quantify the structure or average dissimilarity within the community (Table 1).

Species-based indices
The dissimilarity of one focal invader to the native community can be measured either as the absolute functional (or phylogenetic) difference, or as the ranked difference (Table 1).

To date, most studies attempting to infer invasion processes or anticipate successful invasions have used measures of the absolute functional (or phylogenetic) distance between the invader and the native species (also called 'alpha-niche', Ackerly and Cornwell 2007) (Table 1). These indices are designed to identify situations where invasion success is triggered by an invader's differences from the native species. These differences can be due to species differences in resource use (e.g. the invader exploits resources unused by the natives), but also in predator or parasite attraction (e.g. the invader suffers less from predation than the natives). If all resident species are assumed to contribute to the biotic resistance of the community, an index can be computed as the mean functional distance between the invader and all the native species (MDNS). Alternatively, indices can be computed as distances to a subset of species thought to influence resistance more strongly (e.g. the most abundant natives, or the most similar to the invader). Finally, indices can be weighted by species abundances, under the assumption that abundant species will be more likely to interact with newly introduced species (for a complete review on these indices see Thuiller et al. 2010).

The ranked functional difference between the invader and the native species (i.e. $Trait_{Inv} - \overline{Trait_{Nat}}$; Mayfield and Levine 2010, Kunstler et al. 2012) has recently been proposed as a measure of an invader's competitive advantage over native species (Gallien et al. 2015; Table 1). For instance, in the context of a plant invasion where light is a

Box 1. Elementary guideline for studying invasion processes

When analyzing invasion processes with community ecology approaches many decisions have to be taken to find the methodology that can best answer specific research questions. Here we briefly highlight crucial steps for deciding which index to choose, which dissimilarity estimate (trait vs phylogeny) to rely on, which statistical test to apply and what constraints and which species to consider.

Which index: in order to disentangle environmental filtering, resource opportunity and competitive hierarchy processes potentially involved during invasion, there is yet no single index that can be used (Gallien et al. 2015). Therefore, a combination of absolute (such as MDNS) and ranked difference indices is important (Table 1). Additionally, a recent simulation study has shown that DNNS (Table 1) tends to under-estimate the influence of competitive interactions when both competition and environmental filtering interact (Gallien et al. 2014). Therefore, MDNS or wMDNS (when good estimates of species abundances are available) seem to be the best choices of indices for testing the resource opportunity hypothesis.

Which measures of species dissimilarity: with the growing availability of large phylogenies it is now often feasible to use phylogenetic dissimilarity measures as proxies for functional dissimilarity. However, phylogenetic distances have several shortcomings. First, the use of phylogenetic distances between species implies strong assumptions about the tempo and mode of evolution of the important traits involved in coexistence mechanisms (i.e. that traits evolved with the same rate across all clades of the phylogeny and that there has been no convergent evolution in the traits important for invasion success; Simpson 1944, Webb et al. 2002). Second, they cannot be used to rank species according to their competitive ability, restricting the number of processes that can be tested for. Finally, the use of an aggregate measure of species similarity might be problematic when certain traits influencing the evolutionary history of species are not be involved at all in coexistence mechanisms (e.g. traits related to sexual selection). Using functional distances based on traits that can be clearly linked to species co-existence mechanisms seems therefore more promising in most cases. However, using traits to calculate functional distances also has limitations. For example, in most cases traits are not measured in situ for each species in each community, and instead average trait values (rarely even measured in the study site) are used across communities. Indeed, it has been shown that not accounting for intraspecific trait variability can bias the estimated functional distance between species (Albert et al. 2010). When using traits it might therefore be advisable to at least estimate the sensitivity of the results to intraspecific variability. Depending on the research question, care should also be taken in using trait measurements for the invaders collected in the invaded range, since it has been shown that invasive species can rapidly evolve their functional characteristics during colonization (Leishman et al. 2014, Vandepitte et al. 2014).

Which statistical test: when the aim of the study is to identify the interplay of different processes determining invasion success, the simplest approach is to use regression models. Indeed, regression models can test for quadratic responses in the relationship between invasion success and functional distance, and are less data hungry than complex permutation algorithms. However, if a null model approach is desired for a specific question, we recommend to carefully consider the relevance of applying each of the 4 main randomization constrains: 1) maintaining local community richness and/or the species frequency distribution in the region, 2) maintaining the spatial autocorrelation of abundances, 3) respecting species environmental preferences, 4) maintaining the relative abundance of specific phylogenetic clades. For example, respecting species environmental preferences in the randomization algorithm allows focusing more closely on the effects of biotic interactions.

Which species: a critical step, related to the application of constrains in null model algorithms, is the definition of a reference species pool. When exhaustive lists of species occurring within each community are available (for instance phytosociological relevés for plant communities), it might be more relevant to only use a subset of the resident species in the analyses if the invasive species belong to a specific functional group (e.g. grass, shrub or tree). Indeed, not all species in a community necessarily compete for the same resources, and thus according to the research question it may be more appropriate to compare an invasive grass with native grasses only, and not to the tree species of the communities (Münkemüller et al. 2014). For example in the case of light interception, resource opportunity is probably of prime importance for the coexistence of different growth forms (e.g. herbaceous vs woody species), while competitive ability drives the outcome of assembly between woody species (Kunstler et al. 2012).

limiting resource and the trait under consideration is species height at maturity, then taller invaders (i.e. higher index value) will be more competitive at intercepting light. Such an index can be computed by considering all native species, or just a subset of species depending on case-specific assumptions. These indices differ from the absolute distance indices in that they emphasize the invader's hierarchical position on each trait gradient rather than its average absolute similarity to the community. Note that, as a downside, these indices

cannot be estimated with phylogenetic information (as phylogenetic distances between species are absolute distances).

A number of other species-based metrics commonly used in community ecology have the potential to be adapted to study invasions. For example, the influence of species dissimilarities on regional co-occurrence patterns can be evaluated by correlating 1) co-occurrence indices between a focal invader and each native species (e.g. C-score; Stone and Roberts 1990) with 2) their functional (or phylogenetic)

Table 1. Summary of the main indices proposed in the literature to track invasion processes, their essential assumptions, and key references.

	Name	Description	Assumptions	References
Species-based indices	Absolute difference (MDNS-like) indices	Mean functional (or phylogenetic) distance between the focal invasive species and all (or a subset of) native species.	The considered native species contribute to the biotic resistance of the community.	Schaefer et al. (2011), Park and Potter (2013, 2015a, b), Li et al. (2015a), Marx et al. (2016)
	Ranked difference indices	The standardized mean differences in trait values between the invader and each native species in the community.	All considered species compete for the same limiting resource. The studied functional trait well describes species capacity to compete for the resource.	For an application on native communities see Kunstler et al. (2012), and Gallien et al. (2015) for an application on invaded communities.
	Co-occurrence related indices	Functional (or phylogenetic) distance between the invasive and all native species of the studied region, weighted by their regional co-occurrence score.	Coexistence mechanisms are similar across all communities.	Carboni et al. (2016)
Community-based indices*	MPD-like indices	Mean functional (or phylogenetic) distance between all pairs of species present in the community.	All considered species compete for the same limiting resource(s).	Gerhold et al. (2011), Jucker et al. (2013), Ordonez (2014), Lososová et al. (2015)
	PD_{INV} (vs PD_{NAT})	Sum of all phylogenetic branch length that connect all invasive species in the community.	Species coexisting together over long time scales should be more different than non-coexisting species, due to niche differentiation process.	Cadotte et al. (2010)
	Dark-diversity indices	Ratio of observed and potential community richness.	The greater the potential richness is compared to the observed one, the more intense is the competition. Potential richness can be well estimated.	There are no examples from invasion studies, but see Boulangeat et al. (2012), and Lewis et al. (2016) for applications on native communities.

* The number of community-based indices that can be found in the literature is longer than listed here, but a detailed description of all such indices goes beyond the scope of the present review. We refer to Mouchet et al. (2010), and Tucker et al. (2016) for recent reviews on community-based indices.

distances (Carboni et al. 2016). A pattern of invaders co-occurring with functionally similar native species is consistent with environmental filtering within the region, whereas invaders co-occurring with dissimilar species might indicate that competitive interactions are limiting invasion success locally.

Community-based indices

In the context of invasions, traditional community diversity indices (for a review see Tucker et al. 2016) can be used either to compare invaded vs non-invaded sites, or to assess whether invasive species are filtered by the same processes as the native species. We distinguish here two main types of indices: indices based on the observed community diversity, and indices based on the species that are absent from the community (community dark diversity, sensu Pärtel et al. 2011).

To date many observed community diversity indices have been developed (Tucker et al. 2016), and describing all of them goes beyond the scope of this review. Here we only highlight that each of these indices can measure only one of the three following components of community diversity: 1) richness (e.g. functional richness as the functional space filled by the community), 2) regularity (e.g. functional evenness as the evenness of the abundance distribution in a functional trait space), or 3) divergence (e.g. phylogenetic divergence as the mean phylogenetic distances between the species (MPD); Webb et al. 2002, Villéger et al. 2008). In the context of biological invasions, the functional richness and evenness

components can help identifying resistant communities (Gerhold et al. 2011). For instance, one may ask whether resistant communities tend to be more diverse (e.g. high functional richness) than invaded ones, or dominated by one particular functional group (e.g. low functional evenness). The functional divergence component can complement these questions by identifying whether environmental (e.g. low functional divergence) or competition filtering (e.g. high divergence) among native species influences community resistance to invasion. Finally, community-based indices can also be applied for characterizing the community structure of invasive species within the community, e.g. in order to compare it with the structure of the natives (Cadotte et al. 2010, PD_{INV} and PD_{NAT} in Table 1).

Community dark diversity indices are based on the comparison of observed vs potential richness. Potential richness refers to all species that could occur in the community based on their environmental preferences, but did not succeed due to competitive exclusion (Miller et al. 2009, Pärtel et al. 2011). When competition is an important filter of species coexistence, community potential richness will be larger than the observed richness, since the weakest competitors will be excluded locally. The dark diversity of a site can be estimated through several approaches, such as habitat suitability models (Guisan and Zimmermann 2000) predicting the probability of occurrence for each species in communities based on climatic preferences (Boulangeat et al. 2012, see also Lewis et al. 2016).

Statistical approaches and their limitations

After the calculation of the indices, statistical testing procedures need to be applied to detect whether functional (or phylogenetic) patterns deviate from null expectations. Two main approaches are routinely used: null models and regressions.

Constrained null model randomizations

Using a null model approach has probably been the most common strategy in the analysis of community diversity patterns up to date. In this approach the selected index (see previous section) is compared to a null-distribution obtained through dataset randomizations under a given null-model (i.e. representing expectations of the index value in absence of the process of interest; Gotelli and Graves 1996, Webb et al. 2002). The first step for applying a null model approach is the choice of the randomization procedure. Several algorithms are possible depending on whether the randomizations are manipulating the species occurrence data or the functional (or phylogenetic) distances among species (Hardy 2008). In Table 2 we outline the most commonly used algorithms in invasion ecology and indicate the hypotheses they can test (see more detailed explanation in Supplementary material Appendix 2).

Importantly, several constrains can be applied on the randomization algorithms based on extra information on the studied species or system in order to test more targeted hypotheses (Lessard et al. 2012, Cornell and Harrison 2014). These include (but are not limited to) constrains that: 1) maintain local community richness and/or the species frequency distribution in the region, 2) maintain the spatial autocorrelation of abundances, 3) respect species environmental preferences, and 4) reduce the phylogenetic scale of the analysis.

For example, in most instances randomizations of the species occurrence dataset were constrained in order to 1) maintain at the same time local richness in the sites and the total number of species occurrences in the study area (e.g. Gotelli's 'swap' algorithm; Gotelli 2000, Hardy 2008). Indeed, if rare species have particular functional traits, their frequency in the null communities can otherwise be spuriously inflated. Additionally, 2) if species dispersal limitations are substantial, it would be generally advisable to account for dispersal fields in the randomization algorithm (e.g. species probability of being sampled depending on the distance to the nearest location where it has been detected; Lessard et al. 2012, Warren et al. 2014). Constrained null models that account for dispersal (and other historical contingencies) may also be useful, if contrasted with unconstrained null models, to disentangle the role of neutral processes (e.g. dispersal driven) from niche driven processes (Pigot and Etienne 2015). Further, 3) when both environmental and competition filtering interact, constraining the randomizations by species environmental tolerances will allow to remove most environmental filtering signals and thus more easily detect signals of competition (e.g. weighting species probability of being sampled by the suitability of the environment at the studied site, for instance using habitat suitability models; Chalmandrier et al. 2013). Finally, 4) in cases when species dissimilarity is estimated with phylogenetic distances,

reducing the evolutionary scale of analysis by using a null model that shuffles species only within lineages can prevent confounding effects of convergent evolution among distantly related species (Hardy 2008, Chalmandrier et al. 2013).

Limits to null models and alternatives: regression approaches

While null-models have great potential for revealing non-random patterns in invasions, they suffer from two main limitations (Strong et al. 1984, de Bello 2012). First of all, overly specific hypotheses caused by constraints in the randomization schemes limit null model power. Thus, these analyses must be performed with large datasets (Gotelli and Graves 1996). Second, a single null model can be used to infer one process only, and not multiple interacting processes. Indeed, when compared to null expectations the invaders are either significantly similar or dissimilar from native species. However, if both competition and environmental filtering interplay the invaders are expected to be at the same time not too similar and not too dissimilar from the native species (Gallien et al. 2014). Similarly, a null model approach allows dealing only with one species at a time, whereas we are generally faced with multiple interacting alien species invading multiple communities. To correctly conclude on the dominant processes involved during invasions, one is thus forced to apply several null models (Chalmandrier et al. 2013).

Alternatively, regression approaches can be used to overcome many of the shortcomings of null-models. For instance one can model invasion success and failure as a binary process across invaded and non-invaded communities or across invasive and non-invasive species. The presence or absence of an invasive species is used as the response variable while the value of a functional similarity index calculated for each community is used as the explanatory variable (Maitner et al. 2012, Li et al. 2015a; Fig. 3). If several invaders are analyzed at the same time, species and community identities can be easily included as random factors in hierarchical mixed-effect models (i.e. accounting for the fact that multiple invaders can invade the same communities and each invader can invade multiple communities). Potentially, if several invasive species are expected to interact, joint species distribution models can also be employed to explicitly account for these interactions (Pollock et al. 2014). One additional advantage of regression models is the potential to test for interacting processes by the use of quadratic terms for explanatory variables (e.g. in a quadratic model a negative coefficient for the functional similarity term would be consistent with the interaction of competition and environmental filtering; Fig. 3b; Gallien et al. 2014). Covariates can also be easily included in regressions, allowing consideration of, e.g. environmental gradients and dispersal limitations, without involving the strong loss of power associated with constraints in randomizations.

Seven invasion questions and approaches

We conducted a systematic literature review using ISI – Web of Science (see Fig. 1 and Supplementary material Appendix 1, Table A1 for details) and identified seven key questions in invasion community ecology that have been tackled using

Table 2. Summary of the main (a) standard and (b) constrained randomization procedures available in the literature to provide significance tests.

(a)

	Name	Null hypotheses	Features maintained
Distance matrix	Shuffle species names	The observed invaded assemblage is a random sample of the regional native species pool.	Community structure within sites (richness and evenness); occurrence frequency of each species; spatial autocorrelation of occurrences; invaded site identity; invasive species position on the (functional or phylogenetic) distance matrix.
	Shuffle only alien species names	The observed invader distance to the native assemblage is equal to the distance between any other (random) invader and the native assemblage.	Community structure within sites (richness and evenness); occurrence frequency of each species; spatial autocorrelation of occurrences; invaded site identity; functional (or phylogenetic) composition of native communities.
	Swap an alien with a native species identity	The observed invader distance to the native assemblage is equal to the distance between any (random) species and the native assemblage.	Community structure within sites (richness and evenness); occurrence frequency of each species; spatial autocorrelation of occurrences; invaded site identity; functional (or phylogenetic) composition of native communities.
Species by site matrix	Shuffle presences and absences for each species	The observed assemblages are random samples of regional species pool.	Occurrence frequency of each species; species position on the (functional or phylogenetic) distance matrix.
	Shuffle presence and absence within each site	The observed invaded assemblage is a random sample of native regional species pool.	Community structure within sites (richness and evenness); species position on the (functional or phylogenetic) distance matrix.
	Shuffle presences and absences of each invasive species	The invader distance to the invaded assemblage is the same as the distance between the invader and any non-invaded assemblages.	Community structure within sites (richness and evenness); occurrence frequency of each native species; spatial autocorrelation of native occurrences; species position on the (functional or phylogenetic) distance matrix.
	Swap alien presence with an absent native species, in invaded sites	The invader distance to the assemblage is equal to the distance of any other native species not present in the invaded sites and the assemblage.	Community structure within sites (richness and evenness); occurrence frequency of native species; spatial autocorrelation of native occurrences; invaded site identity; species position on the (functional or phylogenetic) distance matrix.
	Swap invasive and native species names in invaded sites	Invasive and native species have the same distances to the local assemblages.	Community structure within sites (richness and evenness); occurrence frequency of each species; spatial autocorrelation of native occurrences; invaded site identity; species position on the (functional or phylogenetic) distance matrix.

(b)

	Name	Additional features maintained	References
Distance matrix	Only species with similar abundances are permuted	Abundance phylogenetic/functional structure present in the data set.	Hardy 2008
Species by site matrix	Gotelli's swap algorithm	Community richness; occurrence frequency of each species.	Gotelli and Graves 1996, Gotelli 2000, Gotelli and Entsminger 2001
	Torus-translation permutations	Spatial autocorrelation of species occurrences and abundances; occurrence frequency of each species.	Harms et al. 2001
	Species resampling probability increases with geographic proximity from known occurrences	Spatial autocorrelation of species occurrences/abundances.	Boulangeat et al. 2012, Warren et al. 2014
	Species resampling probability increases with species-specific environmental favourability of the sites	Species environmental suitability.	Chalmandrier et al. 2013
	Only species within a lineage or a functional group are permuted	Functional group or phylogenetic lineage belonging.	Chalmandrier et al. 2013, Münkemüller et al. 2014

a functional diversity approach (Fig. 2). Due to the large number of studies and the often inconsistent methodologies, drawing a clear picture from this body of work can be challenging. To overcome this hurdle and provide a benchmark state of knowledge, we tackle each question in turn and highlight its importance in the context of invasion ecology, synthesize and reconcile the often contrasting published results, and propose further perspectives of development (based on the methodological tools described in the previous section).

1) Which species are more invasive?

Identifying which traits make some species more likely to become invasive than others is one of the oldest and most frequently recurring questions in invasion ecology. Invasion success has been shown to be promoted by demographic and competitive traits, such as high fecundity, short juvenile periods, fast relative growth rates, or large height/size (Van Kleunen et al. 2010, Dawson et al. 2011, Richardson
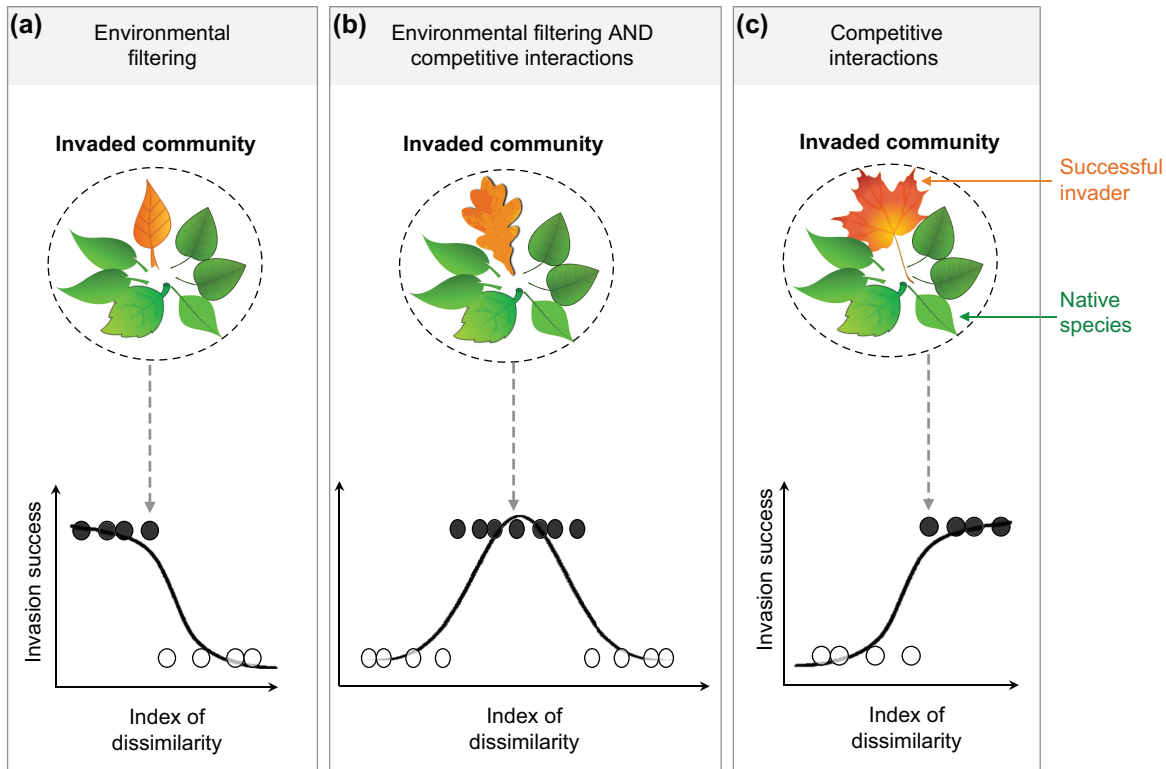
Figure 3. Regression models with (a and c) linear and (b) quadratic terms can refine our understanding of the relationship between species similarity and invasion success. Indeed, for a model predicting species invasion success from a chosen dissimilarity index: (a) a positive linear coefficient suggests that resource opportunity is a driver of invasion success (as the invaders are more successful in communities where they are dissimilar from the other species), while (c) a negative linear coefficient suggests environmental filtering as the main driver of invasion success (as the invaders are more successful in communities where they are similar to the other species). However, (b) if the quadratic term is negative (i.e. hump-shaped) it suggests that both resource opportunity and environmental filtering together are important in invasion success. Closed and open circles indicate invaded and resistant sites respectively. Native and invasive species are represented with green and orange leaves respectively.

and Pyšek 2012, Moodley et al. 2013). Moreover, certain phylogenetic lineages include higher proportions of invasive species than expected by chance, suggesting that phylogenetic relationships can also be useful predictors of invasion success (Lambdon 2008, Cadotte et al. 2009, Novoa et al. 2015). However it is increasingly recognized that successful invasive strategies vary depending on the local environmental context, time period considered and native species pool (Dietz and Edwards 2006). Species-based indices that quantify the similarity between invaders and natives allow accounting for this in the quest for the identification of 'ideal weeds', and of the species at risk of becoming invasive. Here we briefly review studies that have used this functional similarity approach to predict which species are likely to make successful invaders in a region (note that we discuss the studies explicitly focusing on the underlying assembly processes in later sections).

To date, studies investigating species invasiveness as a function of similarity to native species have focused either on establishment success of aliens or on measures of their spread and impact. Most studies have used species-based indices using phylogenetic relatedness as a proxy for functional similarity (see above and Box 1 for discussion on the potential limitations of this approach). The success of introduced species has generally been shown to increase with phylogenetic distance to the native species (Rejmánek 1996 in Californian

grasses, Lockwood et al. 2001 for other plants, and Van Wilgen and Richardson 2011 for North American animal groups). However, studies linking relatedness with invasion spread and impacts have been less conclusive (Schaefer et al. 2011, Park and Potter 2013, vs Ricciardi and Atkinson 2004, Strauss et al. 2006, Tan et al. 2015). This suggests that phylogenetic relatedness could potentially be used to screen for introduced species at risk of becoming established in a region, but will not necessarily also reflect how likely a given species is to spread and have a large impact on the native community.

To date, simply accounting for invader similarity to the native community has not proven enough to generate generalizable conclusions about the potential invasiveness and impacts of newly introduced species. However, further analyses combining both absolute and ranked similarity indices of invasive species to the natives might still help gaining insights on which species might become invasive in the future (Carboni et al. 2016). Specifically, we advocate that promise is held in attempting to link the observed patterns with the underlying processes driving them across environmental gradients, which requires more refined analyses (e.g. environmentally constrained null models), additional data (e.g. environmental measurements), and inclusion of explicit functional trait information in addition to phylogeny, as discussed for questions 3 and 5 and in the perspectives section.

2) Which communities are more resistant to invasion?

Probably the second most investigated question in invasion biology has been whether certain species assemblages are more resistant to invasion than others, and if so why (Fargione and Tilman 2005, De Roy et al. 2013, Kimbro et al. 2013, Longo et al. 2013). Understanding differences between invaded (sensitive) and non-invaded (resistant) sites is crucial for defining management plans that can effectively limit invasion spread at local scales. For instance, one can apply a top-down control of invasion by limiting the propagule pressure by alien species in the most sensitive sites, and/or a bottom-up control by modifying local conditions and thereby improving the resistance of these sites (D'Antonio and Chambers 2006, Young et al. 2009).

By comparing community based indices of invaded vs less invaded communities at different scales, two well-known patterns have been described (see Shea and Chesson 2002 and Fridley et al. 2004 for reviews). On the one hand, at broad spatial scales the number of invasive species generally increases with taxonomic diversity, indicating that sites that offer more resource opportunities for natives do so also for invasive species ('the rich get richer' hypothesis; Davis et al. 2000, Stohlgren et al. 2003, Belote et al. 2008, Parker et al. 2010). On the other hand, at fine spatial scales (or when controlling for varying external constraints) a negative relationship between the diversity of natives and that of invasives is often observed, and is interpreted as invasion resistance by native species through priority and complementarity effects (Elton 1958, Naeem et al. 2000, Fridley et al. 2004, Fargione and Tilman 2005, Ricotta et al. 2010). More recently functional and phylogenetic diversity of native communities have been recognized as potentially more informative metrics to infer community resistance, as they are more likely to correlate with occupied niches in the community and fewer available resources for an invading species (Maron and Marler 2007). Independent observations in natural and experimental systems have in fact shown that community resistance to invasion tends to increase when native species are highly phylogenetically diverse (Gerhold et al. 2011, Fridley and Sax 2014), and functionally similar to invaders (Young et al. 2009, Hooper and Dukes 2010, Price and Pärtel 2013). In contrast, most studies exploring the effects of phylogenetic relatedness between invasives and natives on community resistance (i.e. phylogenetic species-based indices) have yielded mixed (Jones et al. 2013, Liu et al. 2014, Poe 2014, Lososová et al. 2015, Marx et al. 2016) or non-significant results (Castro et al. 2014, Fleming et al. 2015). Nevertheless, a recent study by Tan et al. (2015) in a manipulative experiment with bacterial assemblages found evidence that phylogenetic relatedness to invaders was a better predictor of biotic resistance than the phylogenetic diversity of the community.

Contrasting observed communities that are sensitive vs resistant to invasion by using a combination of community-based and species-based indices should be pursued further to confirm these observations. In particular, long-term experimental studies (Prieur-Richard et al. 2000, Maron and Marler 2007, Hooper and Dukes 2010, Byun et al. 2013) have the clear advantage of allowing the causes and effects of invasion to be teased apart, an issue that can be very challenging with observational data (Gerhold et al. 2011, Jucker et al. 2013, Bennett et al. 2014, Marcantonio et al. 2014, Lapiedra et al. 2015). As proposed in question 1, in order to gain a more mechanistic understanding of the drivers of biotic resistance, future studies should focus on better linking community patterns with the processes driving species coexistence (question 3).

3) Which processes drive coexistence between invasive and native species?

As described in the previous sections, functional or phylogenetic similarity indices can be used to predict the success of potential invaders or the resistance of native communities. However, by linking these patterns with hypotheses on the underlying processes driving species coexistence many more insights can be gained (Darwin 1859). Indeed, quantifying the relative importance of environmental, biotic or neutral processes is 1) crucial to be able to efficiently manage invasions in a specific region, as well as 2) an opportunity to better understand the ecological mechanisms that shape community assembly and species coexistence.

In recent years a growing number of studies have used species-based similarity indices to infer the dominant processes of invasion at a variety of spatial scales. Darwin's expectations on the importance of environmental filtering have often found support at regional scales, with invasion success increasing in the presence of native congeners (e.g. for invasive plants, reptiles and fish, Daehler 2001, Duncan and Williams 2002, Ferreira et al. 2012, Allen et al. 2013), or of closely related species in the native species pool (e.g. for invasive plants and birds, Maitner et al. 2012, Park and Potter 2015a, b). Nonetheless, in at least two case studies the presence of native congeners was shown to have only a weak effect on invasion success (for invasive plants and fish, Lambdon and Hulme 2006, Ricciardi and Mottiar 2006) suggesting rather a weak influence of the environment in filtering invasive species. Moreover, two other case studies in the Southern Hemisphere concluded that competition was involved in filtering invaders regionally given that invasion success was found to increase with phylogenetic (invasive plants, Bezeng et al. 2015) and functional distances to natives (invasive fish, Skóra et al. 2015). Patterns such as these – which are consistent with the signature of competitive interactions – have been observed much more commonly at local scales, where invasive species have generally been found to have higher establishment success when they were functionally (Petermann et al. 2010, Price and Pärtel 2013) or phylogenetically distant from natives (e.g. for invasive plants and bacteria, Jiang et al. 2010, Davies et al. 2011, Ramos et al. 2014, Li et al. 2015a). In summary, though there have been exceptions (Proches et al. 2015), the results from local scale studies relying on species-based absolute similarity indices generally suggest that competitive interactions and resource opportunities are important in limiting invasions within local communities. Nevertheless, more complex interactions between native and invasive species have additionally been shown to affect invasion patterns. Indeed, competition for shared pollinators (Burns et al. 2011) and escape from

predation pressure (Hill and Kotanen 2011) have both been found to promote local scale patterns of functional dissimilarity between invasive and natives species. Lastly, there have only been a handful of studies that have tested the competitive superiority hypothesis with species-based ranked functional similarity indices, and their mixed results do not yet allow drawing general conclusions (Gallien et al. 2015, Gross et al. 2015).

Overall, compiling results from previous studies supports the hypothesis that environmental filtering of invasion success is generally most evident at coarse spatial resolutions, while competitive interactions between invasive and native species leave a more pronounced signature in trait patterns at local scales (Carboni et al. 2013, but see also Strecker and Olden 2014). Our review also highlights three important aspects of coexistence that we believe have received too little attention. On the one hand, resource opportunity and competitive exclusion are rarely disentangled (for instance by using both absolute and ranked functional similarity indices; but see Gallien et al. 2015, Gross et al. 2015). However this distinction seems crucial as it would allow distinguishing invasive species that tend to be more opportunists (or ruderals) from species that are instead more competitive. On the other hand, the relative importance of environmental filtering, competition and their interaction for invasion success is rarely estimated. Indeed, because invasive species usually spread over heterogeneous landscapes, at the community-scale the relative importance of environmental filtering and competition for invasion success may vary along environmental gradients (see question 5). Finally, although eco-evolutionary neutral processes have been shown to fundamentally alter the structure of communities (Pigot and Etienne 2015), the relative influence of neutral versus niche-based processes is seldom addressed when studying invasion patterns. We suggest that future studies addressing the processes driving invasion should account for these aspects.

4) Do the processes driving invasion change with species invasion stage?

In order to become invasive sensu stricto, introduced species have to survive a series of stages along the so-called introduction-naturalization-invasion continuum (Richardson and Pyšek 2012). The relative importance of different processes affecting a species' survival may change along this continuum. For instance, the survival of recently introduced species may be highly influenced by propagule pressure, naturalized species may be more influenced by climatic suitability and reproductive characteristics, while invasive species (sensu stricto) may be primarily influenced by their dispersal and competition traits (Dietz and Edwards 2006, Theoharides and Dukes 2007, Richardson and Pyšek 2012). Understanding whether and how these processes change along this continuum is therefore crucial to adjust management and eradication strategies, and identify sites most at risk of invasion.

To date relatively few studies have used a functional similarity approach to explicitly test for changing processes along the invasion stage continuum, despite the fact that species- and community-based similarity indices seem extremely well suited for this task. For example, Diez et al. (2008) found that the influence of native congeners on non-native plant species depended on the invasion stage considered. Pellock et al. (2013) also compared how the probability of first becoming naturalized and then invasive depended on numbers of congeneric plant species in native communities. They concluded that the importance of competition and resource opportunities for alien species was significantly higher at early stages of invasion than at later ones. Given the limited number of studies, this question seems to deserve further attention in the future, potentially focusing on testing a larger variety of coexistence mechanisms at each stage.

Future observational studies could compare aliens known to be at different stages in specific regions (Pellock et al. 2013, Carboni et al. 2016) using species-based indices and combinations of null models to infer the relative importance of environmental filtering, competition and neutral processes in each stage. In this context, dark-diversity indices may be of additional interest to estimate the general intensity of competition at the community scale (e.g. testing whether competition intensity increases with species' invasion stage). Attempting to draw conclusions by synthesizing results of previous studies, which have addressed each stage independently, is challenging and requires the application of rigorous meta-analytical methods, which goes beyond the scope of this review. However this seems another promising avenue in order to fill this gap and search for a general answer to this question.

5) Do the processes driving invasion vary along environmental gradients?

The processes influencing invasion success are also very likely to vary along environmental gradients associated with variation in abiotic stress, productivity or disturbance (Perelman et al. 2007). For example, ecological theory predicts a weaker influence of competition on co-existence in less productive communities (Grime 1973, 1977, but see Goldberg et al. 1999). Therefore along a productivity gradient, the competition between an incoming invasive species and the resident natives can be expected to be comparably more important in highly productive environments. Similarly, the stress-gradient-hypothesis (Callaway and Walker 1997) predicts a shift in the importance of environmental filtering and competition along a stress gradient. Consequently, the influence of environmental filtering is expected to be stronger at the edges of an invader's ecological niche in extreme environmental conditions (e.g. very cold or very warm), whereas competition may be a stronger impediment to successful invasion in less stressful conditions (von Holle 2013). By contrast, along a disturbance gradient (e.g. where resource fluctuation increases) ruderal invaders (sensu Grime 2001) can be expected to be more successful in the most disturbed sites (Davis et al. 2000), since environmental fluctuations are expected to reduce the effects of interspecific competition (Chesson 2000). Therefore, one can expect the pressure of introduced propagules to become increasingly important in determining the successful establishment of introduced species when disturbance frequency increases (Davis et al. 2000).

A number of studies in invasion community ecology have attempted to track how the relative importance of different processes changes along environmental gradients using a functional similarity approach. Results have been mixed: on the one hand, focusing on biotic resistance Maron and Marler (2007) found that native plant functional diversity provided strong invasion resistance even after experimentally inducing high resource availability through addition of water, suggesting a weak link between competition experienced by invaders and resource availability. On the other hand, Cleland et al. (2011) found that nitrogen enrichment did not alter the patterns of similarity between successful invasive species and the native community. Similarly, Dante et al. (2013) found no influence of productivity (and resource variation) on the degree of flowering overlap among coexisting native and alien plant species in an old-field plant community. Finally, Gallien et al. (2015) studied the change in relative importance of invasion processes along alpine environmental gradients but found no evidence of competitive interactions varying consistently on these gradients. Overall, these findings highlight the potential of studying and comparing functional similarity patterns of invaders along gradients, but also indicate that clear evidence linking a change in the importance of different processes to shifting environmental conditions is still limited and often contradictory (with the exception perhaps of the link with disturbance). Much more needs to be done to answer this question, and both experiments manipulating stress or resource levels and observational studies analyzing invaders similarity patterns across gradients are still needed. Interactions between the functional similarity of invaders to the native community and environmental gradients can then be examined by adopting a regression approach to model invasion success, as this allows to flexibly cope with continuous gradients (such as climatic, productivity or disturbance gradients).

6) Do invasive species coexist with the natives via the same processes that rule native species coexistence?

The drivers of invasion success can vary along environmental gradients, but do they follow the same trends as the drivers of native species coexistence along these gradients? For instance, are invaders limited by competitive interactions only in communities where native species are also strongly filtered by biotic interactions? Can invasive species coexist with native species in highly competitive communities due to high propagule pressure even though they are bad competitors (Simberloff 2009, Kempel et al. 2013)? These questions are intriguing, and addressing them could improve our ability to predict the likely impacts of invasive species on native communities. However, native species coexistence and the coexistence between natives and invasive species have largely been studied independently of one another (but see below for a few examples).

A small number of studies have tackled these questions, with limited congruency among their results. For example, Cadotte et al. (2010) found that exotic species were phylogenetically clustered in Californian plant communities, suggesting environmental filtering, while native species

tended to be overdispersed, suggesting filtering by competition, (similar results were found by Carvallo et al. 2014). On the contrary, in a worldwide set of plant communities Ordonez (2014) showed that invasive species were more functionally distant from the native community than natives were among themselves, and suggested that invasion tends to occur via resource opportunity while native species tend to be filtered by local environmental conditions. In contrast, two other studies found instead that the functional or phylogenetic similarity to the rest of the community did not depend on species status as invasive or native, suggesting that all species were filtered by the same processes (Emery 2007, Lemoine et al. 2015). Finally, a meta-analysis by Parker et al. (2011) revealed that introduced pest species were less related to recipient communities than non-pest species, independently of whether they were exotic or native.

In sum, previous studies have shown contradictory results. In an attempt to settle this discrepancy, Leffler et al. (2014) recently conducted a meta-analysis and found very limited evidence that exotic invasive species were more functionally dissimilar from the resident natives than co-occurring native species were among themselves. Based on these results, Leffler et al. (2014) suggested that differences in trait values between alien and native species might actually have limited power to predict invasion success. However their view has been challenged and has spurred further debate (Leffler et al. 2014, 2015, Dawson et al. 2015), suggesting that future research will continue to address this question. Overall, the potential differences in drivers of coexistence among invasive and native species raises the question of whether invasive species have a specific 'invasive' behavior in the invaded ranges, or whether they behave exactly as they normally do in their native ranges (see question 7).

7) Are invasive species filtered by similar processes in their native and invaded ranges?

Some species are known to be sparsely distributed in their native range, but to become highly invasive in a new region due to the absence of natural enemies (Van Kleunen et al. 2010), increased performance (Parker et al. 2013), or because they carry novel weapons (Vilcinskas et al. 2013). Nonetheless, it is rarely tested whether differences in coexistence mechanisms between the native and the invaded range can also explain invasion success (Hierro et al. 2005, Van Kleunen et al. 2010). Such a comparison is however crucial to understand if invaders 'do something different' in recipient communities that enables them to attain such dominance (Hierro et al. 2005). For instance, release from natural enemies might make invasive species much more competitive in the invaded range than at home. Alternatively, aliens might profit from resources that are less used by resident species in the invaded range than in their own native range, so that resource opportunity might emerge as a stronger driving process of success in the new region.

Surprisingly, this question has been poorly addressed in invasion community ecology using a functional similarity approach. A first attempt was recently made by Nahrung and Swain (2015), who compared eucalypt specialist insects that have become pests in Australian plantations (natives) to

those that have established overseas (invaders) in terms of their traits and found that overall aliens and native colonizers differed significantly. Another recent study by Escoriza and Ruhí (2016) on two well-known invasive amphibian species, the bullfrog and the cane toad, showed that these invasive species were more functionally distant from the native species in the invaded areas than in their native ranges. More work in this direction is clearly required to identify and quantify potential changes in coexistence mechanisms of invasive species within communities between their native and invaded ranges. For example, in order to identify differences between native and invaded regions, future studies could compare the functional similarity between a focal invasive species and the species with which it coexists in both its native and invaded ranges (e.g. using species-based indices in combination with dispersal constrained null models).

Perspectives for invasion and community ecology

After reviewing the recent works adopting a functional similarity approach to answer the seven questions described above we conclude that our general understanding of the processes regulating invasions remains partial for two main reasons. On the one hand, for several questions the limited number of both empirical and experimental case studies hampers the generalization of results. On the other hand, the use of functional similarity indices simplifies a process that is in reality highly complex. Invasion processes are simplified 1) because invasion success is in fact composed of a sum of demographic components that can be differently affected by native community structure, 2) because facilitation, and 3) multi-trophic interactions between invasive and native species are usually ignored, and 4) because the impacts of invasive species on native communities are neglected. Nonetheless, combining the traditional functional similarity approach with new conceptual and methodological tools currently developed in the fields of community ecology, population ecology, and network science will help integrating this complexity. In the following section we develop four perspectives that we believe are the most promising avenues for the next generation of invasion community ecology studies.

1) Integrating demographic rates in invasion community ecology

A large part of the studies using a functional similarity approach to investigate invasion processes focuses on the general drivers of invasive species presences (or abundances) and absences. However, the presence and persistence of an invader is determined by three important demographic stages: its 1) recruitment, 2) growth, and 3) survival rates in the community. Up to date little is known on the actual influence of the native community on each of these demographic rates. Yet, the more traditional functional similarity approach could be adapted to infer what specific demographic phase is most affected e.g. by environmental filtering or competitive interactions. Are specific invaders absent because of low recruitment, low fecundity, high mortality, or a combination of these demographic characteristics? Indeed it has been

shown that phylogenetic relatedness can have contrasting effects on different life-stages of invading species (Li et al. 2015b). By relating invasive species demographic rates with the functional or phylogenetic distance between invasive and resident native species (e.g. with regression models), the critical life stage driving invasion patterns can be identified. For instance, investigating the influence of competitive interactions on each demographic rate would improve our understanding of community biotic resistance (question 3), and of the more specific mechanisms that foster exotic species across their invasion stages (question 4). Experimental studies explicitly manipulating the functional and phylogenetic structure of communities would be well suited to investigate these questions as they allow thorough measurements of recruitment, growth and survival through time (Li et al. 2015b). Alternatively, very detailed field measurements can be used to estimate demographic parameters (Godoy et al. 2014, Kraft et al. 2015). Since species demographic rates are known to also vary along niche gradients (Angert et al. 2009, Thuiller et al. 2014, Pironon et al. 2015), it might be important to also manipulate environmental conditions (experimental) or account for local environmental variation of the studied sites using covariates (observational). Such fine understanding of the effect of coexistence mechanisms on invasive species abundances may further be employed to predict the areas that can be at highest risk of invasion, for instance areas of high recruitment and low mortality rates, allowing to design more targeted management and prevention measures (Li et al. 2015b).

2) Integrating facilitation mechanisms in invasion community ecology

Up to date biotic interactions have mostly been considered in the study of plant invasions in terms of negative interactions (i.e. competition), while the potential positive interactions with resident native species (i.e. mutualism and facilitation) have generally been neglected (Traveset and Richardson 2014). However, recently manipulative experiments (Zarnetske et al. 2013, Gross et al. 2015) and analyses of time series (Martorell and Freckleton 2014) have shown that facilitative interactions can be an important and largely underestimated component in invasion processes (see also Kuebbing and Nuñez 2015). Facilitation can be important among invasive species (i.e. invasional meltdown; Flory and Bauer 2014), but can also occur between invasive and native species, where the invader may act as either the facilitated (Becerra and Bustamante 2011, Wundrow et al. 2012, Madrigal-González et al. 2013) or even the facilitating species (Sun et al. 2013, Traveset and Richardson 2014). Moreover the relative importance of competition and facilitation for invasion is likely to vary along gradients as well. For example von Holle (2013) showed that at the community scale facilitative interactions between native community members and invaders were more dominant in environmentally stressful sites, while invaders experienced greater competition in less stressful areas (as predicted by the stress-gradient-hypothesis; Callaway and Walker 1997).

There are two main reasons for the neglect of facilitative interactions in invasion community ecology up to date.

While the first one is essentially historical, given that invasive species are fundamentally studied because of their negative effects on native biotas, the second one is methodological, since there is yet no consensus on the appropriate tools for identifying and quantifying facilitative interactions based on observed functional community patterns (but see Santoro et al. 2012, von Holle 2013). Classically, patterns of species co-occurrence have been used in community ecology to infer the prevalence of facilitative mechanisms (Santoro et al. 2012). Similarly, in the case of invasions it may be possible to infer whether an invasive species is facilitated, for instance by studying if it co-occurs with a native species more often than expected by chance (after accounting for environmental filtering), or if it is significantly more abundant where the native is present than where it is absent. However it is unclear whether facilitation between invasive and native species is mediated by high or low functional (or phylogenetic) similarities between the species. More in general, there are much less clear hypotheses relating functional similarity of co-existing species with facilitative processes (but see McIntire and Fajardo 2014). One might hypothesize that native species might facilitate invasive species with similar functional traits (e.g. flowering phenology) via pollination services for instance. By contrast one could also expect greater facilitation of functionally distinct alien species if for example benefactor native species promote the establishment of aliens by providing shade or via hydraulic uplift. Before functional similarity patterns can be used concretely to study facilitative mechanisms tests of such hypotheses are critically needed.

3) Integrating multi-trophic interactions into invasion community ecology

Many introduced species rely on multi-trophic mutualisms in their new habitats to become naturalized (Traveset and Richardson 2014). Mutualisms can be important at all stages of the introduction-naturalization-invasion continuum: 1) for establishment via symbioses between plant roots and microbiota (Pringle et al. 2009, Dickie et al. 2010, Rodríguez-Echeverría 2010, Bennett 2013) or plant–ant protection (Ness et al. 2013), 2) for reproduction via animal-mediated pollination (Burns et al. 2011), and 3) for dispersal via animal seed dispersers (Sun et al. 2013, Traveset and Richardson 2014). Invasive species may also benefit from predator or parasite release in the invaded ranges (Van Kleunen et al. 2010, Hill and Kotanen 2011, but see Levine et al. 2004), or compete with the native species via the sharing of mutualistic partners (Burns et al. 2011, Gibson et al. 2012). However, up to date ecologists focusing on functional similarity patterns have generally restricted their analyses on processes regulating coexistence within single trophic levels.

One promising avenue to integrate multi-trophic interactions in invasion community ecology is to compare the similarity of focal species sharing the same trophic level (e.g. invasive and native plants) in their associated species on other trophic levels (e.g. native herbivores; Morlon et al. 2014). For instance, in a plant invasion context, it is possible to identify the number of shared herbivores between a focal invader and each native plant species in the community (e.g.

through the Jaccard index). One can quantify if the invader suffers from a particularly high or low number of herbivores (or a high vs low functional diversity of herbivores) compared to the other plant species in the community by using a species-based similarity index (e.g. MDNS) and a null model (e.g. shuffling the predator–prey links among the species). Further, from a more functional perspective, one can also compare the functional diversity of the invader's predators or seed dispersers with the diversity of native species' predators or seed dispersers. Such an approach would allow to assess the importance of the 'enemy release hypothesis' for invasion success in general, but also to address more specific questions such as whether few common generalist predators or rather many different frugivore specialists can hamper invasions. Another way to integrate multi-trophic interactions in community ecology is to study the functional co-variation of the traits of species in one trophic level (e.g. fleshy fruits plants: fruit size and length) with the functional characteristics of species in another trophic level (e.g. frugivore birds: beak size and breadth; Dehling et al. 2014). Dehling et al. (2014) used this approach through RLQ analysis (Dray and Legendre 2008) to highlight how traits of frugivore birds were associated with characteristics of their food resource along an altitudinal gradient in the Andes. In the context of invasion ecology, such an approach would be particularly interesting for example to identify which traits of seed dispersers or herbivores are associated with successful invasive species.

4) Integrating the impacts of invasive species on native species

The great majority of studies using a functional similarity approach in invasion community ecology have been directed at inferring the drivers of successful invasions. However, invasive species' presence can also alter the structure of native communities, sometimes with cascading impacts (Winter et al. 2009, Jucker et al. 2013, Bennett et al. 2014, Kuebbing et al. 2014, Gooden and French 2015). From a theoretical perspective, an invader will be more likely to affect its recipient community when it can 1) decrease local native species abundances (e.g. the invader is a better competitor than the native species, and not only present due to resource opportunities), 2) increase the abundance of some local native species (e.g. the invader provides a new resource to the system), and/or 3) modify the local environmental conditions in a way that favors its growth over native species, or 4) in a way that favors the establishment of other invasive species (e.g. by increasing the local suitability of the site, such as positive feed-backs of nitrogen fixing species; Simberloff and Holle 1999, see also Richardson et al. 2000, MacDougall et al. 2009). Regarding invasive species impacts on native species, Aizen et al. (2008) have for example shown that during invasions, alien species can shape network structures, usurping links to generalist natives. On the contrary, some invasive plants can provide a key service to native specialist pollinators (Stouffer et al. 2014) and some introduced birds can supply fundamental dispersal services (Foster and Robinson 2007). Regarding invasive species influences on other alien species, the 'invasional meltdown' hypothesis proposes that

the establishment of one invasive species in a community may facilitate the establishment of further invasive species. In fact a newly established alien may favor newcomers by altering the local biotic interaction dynamics (O'Dowd et al. 2003, Grosholz 2005, Green et al. 2011, Prior et al. 2015), or by modifying the local abiotic environment (e.g. increasing nitrogen availability, soil salinity or fire frequency; Simberloff and Holle 1999). Although this idea is crucial for elaborating multi-invader management actions, and anticipating invasion impacts over time, the prevalence and importance of invasional meltdown phenomenon in nature still remains unclear.

Functional (or phylogenetic) diversity approaches can then be used to infer whether invaders are passengers or drivers of community structure (Gerhold et al. 2011, Bennett et al. 2014, Burns 2014), whether their impacts vary with their functional similarity to the native species (as shown by Ricciardi and Atkinson 2004), and whether they are leading to functional homogenization of native communities (Winter et al. 2009). Potentially, three types of studies would allow disentangling causes and effects when relating invasions with functional similarity to the natives. Ideally, long-term monitoring, in the field or under controlled experimental settings, and time-series data are needed in order to assess changes in community composition over time. In the absence of long time-series, re-visitation of historical community plots available through data-bases may be the best strategy to assess community change (Chytrý et al. 2014). By establishing paired plots of invaded and non-invaded communities when revisiting historical plots, one can disentangle community structure changes induced by invasive species colonization vs. background changes due to human disturbance or climate change. Finally experimental manipulations under controlled conditions can help understanding changes in community structure brought about by invasions.

Concluding remarks

By reviewing the literature we identified a number of generally consistent patterns in the relationship between species functional similarity and invasion success. For example, at large spatial scales phylogenetic relatedness of invasive and native species is a good predictor of invasion success, but a poor predictor of invasion impacts. At fine spatial scales, community resistance to invasion tends to increase with native species diversity and with similarity to the invaders, consistent with patterns emerging from biotic interactions. This synthesis highlighted that the functional similarity approach holds promise for understanding and predicting invasions over large extents. Nevertheless, we also concluded that our general understanding still remains partial for many important questions in invasion community ecology, either because they have been yet poorly addressed or because of methodological shortcomings of the approach as adopted to date. In particular the application of modern regression approaches (such as hierarchical modeling and joint species distribution modeling), as well as the integration of complementary indices will allow to better disentangle resource opportunities, competitive exclusion and neutral processes, and help overcoming some of the previous limitations. In addition to these methodological aspects, we advocate that the way forward lies in integrating observational and experimental analyses and in explicitly considering species' demographic rates as well as complex biotic interactions. We conclude that, if applied correctly and complemented through new advances in ecological research, the functional similarity approach still offers many opportunities to enhance our understanding of biological invasions.

Summary points

1) Using a combination of species-based indices (focusing on absolute and ranked functional similarity to the natives) allows inferring the relative influence of environmental filtering, competition, and resource opportunity as potential filters regulating coexistence between invasive and native species.

2) In this functional similarity approach, null models or regression models can be used to assess deviations from random patterns. Constrains or covariables should be used to account for differences e.g. in propagule pressure or environmental preferences among species.

3) Regression models are best suited for detecting multiple processes when they interact, because they allow testing for quadratic responses.

4) Functional traits are better suited than phylogenetic relatedness for a precise understanding of coexistence mechanisms between aliens and natives. If possible, the influence of intraspecific variability should be assessed.

5) Among the seven main questions addressed in invasion community ecology with functional similarity approaches, only few have received clear answers. Major trends remain to be identified on whether the main processes filtering species colonizing new communities: a) depend on the invasion stage considered, b) vary along environmental gradients, c) change in the introduced range compared to the native one, and d) are fundamentally different for invasive species compared to native ones.

6) Further interaction mechanisms should be considered in invasion community ecology, such as facilitative and multi-trophic interactions.

7) The influences of different filtering processes on invasive species demographic rates remain largely unexplored.

8) To understand the causes and consequences of invasion better combinations of observational and experimental analyses are needed. Observational analyses can be used to generate hypotheses on coexistence mechanisms in species rich systems, while experiments can then be used to validate these hypotheses on a reduced set of carefully selected species.

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