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Optimal differentiation to the edge of trait space (EoTS)

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Abstract

The ecological and evolutionary processes that allow alien species to establish and dominate native communities (i.e., become invasive) have been a rich area of research. Past areas of inquiry have included identifying the traits necessary to invade a community and/or determining how phylogenetic relatedness of the introduced species with the resident community can promote invasive success. Yet despite decades of research, little consensus exists about why particular species successfully invade native communities while others do not. Here we develop a conceptual framework for why only certain introduced species become invasive: optimal differentiation to the edge of trait space (EoTS). We posit that optimal differentiation leading to successful invasion into a community requires that the multi-dimensional trait space of the introduced species exists at the edge of the multi-dimensional trait space of the native community. Species that possess traits that are too different cannot enter the community because of environmental filtering, while species that are too similar will either become integrated into the community but not take over or alternatively never establish. We apply this conceptual framework to species functional traits and discuss how both genetic processes and phylogenetic processes may also result in optimal differentiation to EoTS.

Keywords Admixture · Biological invasions · Community organization · Functional traits · Optimal differentiation · Phylogeny

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Introduction

The introduction of species that are not native to the community can provide insights into the way that ecological and evolutionary processes interact across levels of biological organization (Sax et al. 2005). Yet the invasion process whereby a new species can take over a well-established community has parallels in several disparate fields of study. For example, why does one song become a multi-platinum hit whereas other similar songs fade rapidly into obscurity (Ordanini et al. 2018)? Why are some scientific contributions cited thousands of times while others are barely cited (Uzzi et al. 2013)? Why do some seemingly similar businesses become global success stories while others that produce similar products and services barely survive? These seemingly different phenomena may be explained by a concept called *optimal differentiation (*Auskin and Mauskapf 2017*)*. Successful insertion of a new player in both biological and social contexts may be related to the degree of differentiation of the new player from the current state of the system. For example, in business, highly successful start-ups are often termed "disruptors" that tackle the same commercial opportunity as other established businesses but incorporate a new strategy (Leinwand and Mainardi 2016). In music, songs that sound too similar languish while songs that contain original features become hits (Ordanini et al. 2018). The concept of optimal differentiation assumes that the state of a system can be predefined by metrics that quantify the dispersion of new entities from the existing entities. Consequently, the level of optimal differentiation of a new entity should be defined in relation to the current state of the system, and not in any absolute sense.

Applying the concept of optimal differentiation to species introduced into the community means that successful invasive species may require traits that are similar enough to the resident species in the existing community so they can successfully pass through standing environmental filters to establish (Richardson et al. 2000) but just different enough from the existing community that the species can exploit an open or underutilized niche (Abrams 1983). Thus, the degree of differentiation that allows an introduced species to take over a community requires that the species has traits that put it at the edge of the resident community trait space (i.e., Edge of Trait Space (EoTS; sensu Divíšek et al. 2018). This is the result of a balancing act—conforming to the community trait norms to survive environmental filtering (Kraft et al. 2015) but avoiding intense competition from limiting similarity through niche differentiation (Abrams 1983). The concept of EoTS allows us to extend the concept of *optimal differentiation* to provide a metric that predicts the degree of differentiation required for an introduced species (or song or business) to infiltrate a community, and potentially take it over. For any community, we can locate all current species of the community in the multidimensional trait space and compute the field intensity based on trait-mediated interactions (akin to the gravitational field). The field intensity thus allows us to identify the centroid and periphery of the sphere of influence of the community. Next, we can compute the trait distribution for an introduced species and estimate its establishment trajectory, based on the distances in the multidimensional trait space between the introduced species and the native community. Consequently, the relative position of an introduced species in the trait space provides a metric to determine its fate after introduction (fails to establish, establishes but does not dominate (i.e. naturalizes), establishes and dominates (i.e. invasive). The metric provides a way to compare the trait distribution of the native community with the traits of the introduced species and thus,

to determine the position of the introduced species in the trait space relative to the native community (Divíšek et. al. 2018).

Besides providing a prediction about the traits necessary to invade a community (Divíšek et al. 2018), the EoTS concept can be extended to lower levels of biological organization (i.e. genome) and higher levels of biological organization (i.e. phylogeny). At lower levels, genetic processes that increase genetic separation but provide some coherence (i.e. admixture) may create functional trait profiles that are at the EoTS. At higher levels, species that are too closely related to the existing species in the community may be unable to establish into a community but species that are too distantly related may lack the traits necessary to survive. In this context, EoTS echoes Darwin's (1859) naturalization hypothesis that introduced species closely related to the established species would fail to invade because their trait profiles would be too similar. In the EoTS hypothesis, we posit there exists an optimal degree of phylogenetic distance that promotes invasion. We further hypothesize that the concept of EoTS should be self-similar at the three levels of biological organization.

In the remainder of the essay, we further develop the concept of EoTS and discuss how to construct the EoTS profile for a community and discuss the application of the EoTS to the three levels of biological organization. Our goal is to explore the EoTS across the spectrum of biological organization and discuss some ways that the concept might be tested in the future with the hope that the concept opens some new avenues of research.

EoTS definition and construction

We construct the EoTS in terms of centroid versus periphery in the functional trait space defined by the trait dispersion of the residing species of a community (Fig. 1a). Functional traits are defined as the morphological, biochemical, physiological, structural, phenological or behavioral characteristics of an organism that constitute a response of the organism to its environment, and which may provide a fitness advantage (Díaz et al. 2013). The trait profile of a community refers to the gradient field in the multi-dimensional functional trait space calculated using centrality metrics based on each resident species' functional trait position and demographic features (e.g., abundance). Although many such metrics are available (e.g. Divíšek et al. 2018; Hui et al. 2021), their strength and weakness for this purpose warrant further attention. It is the position of the multi-dimensional trait profile of the introduced species within the community trait profile that provides the rationale for the EoTS.

Functional trait space and the EoTS

Introduced species can follow different fates after introduction; some fail to establish, some remain present at low density, others proliferate and become more fully integrated into the community, and others (a small sample) are able to become dominant, potentially causing massive ecosystem transformation (Richardson et al. 2000; Gaertner et al. 2014). Successful invasion into a new community may require species to have different traits than those of the native resident community (Ordonez et al. 2010; van Kleunen et al. 2010; Tecco et al. 2010; Cadotte et al. 2018; Hui et al. 2021), but the alternative is also possible (Leffler et al. 2014). Tecco et al. (2010) pose the problem as a dichotomy: Should introduced species "join the locals" or "try harder"? Their results show that which strategy is successful depends upon the life form with herbaceous plants joining the locals and woody plants
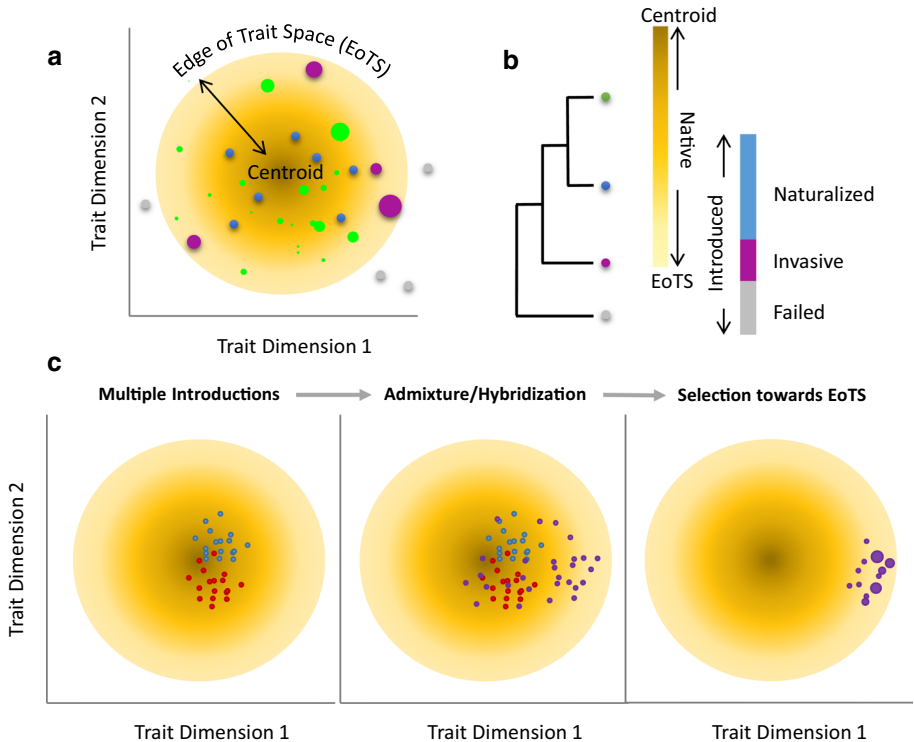
Fig. 1 **a** Panel a depicts a two-dimensional trait space. The dark area in the center represents the centroid of the community distribution; the colored dots represent the position of populations of different species in the community in the two-dimensional space: Green dots represent resident species in the community, with the size reflecting relative abundance; grey dots represent introduced species that failed to establish; blue dots represent species that are introduced and become naturalized; purple dots represent species that are introduced and become invasive. The relative size of the dots indicates the population size. **b** Panel b depicts the phylogenetic relatedness and position along the two-dimensional trait axes for introduced species across a range of different potential outcomes: naturalized, invasive and failed to establish along with the hypothesized phylogenetic relatedness of the species. For example, failed species (those that did not establish into the community) are outside the current EoTS of the community trait distribution and are more distantly related. **c** Panel c depicts how mating between distinct populations following their introduction into a community can create a population with distinct trait profiles that, following subsequent selection, reside at the EoTS. The left most panel: blue and red dots signify geographically distinct populations introduced into the new range and their position in the two-dimensional trait space; the middle panel represents the admixture of the two distinct populations in the introduced range (purple dots); the right-most panel: admixed individuals with traits at the EoTS in the introduced range are, according to this model, destined to become invasive.

trying harder. Yet the conceptualization of optimal differentiation to EoTS can resolve this paradox because introduced species need to be just different enough to become invasive. For example, Divíšek et al. (2018) found that across six distinct temperate communities in central Europe, naturalized species (non-native species in the community) had traits that were similar to the trait profiles of the native community whereas invasive species (non-native species that dominate the community) had trait profiles that were at the edge of the trait profile of the existing plant community. The concept of EoTS also resolves another long-standing controversy; that is, whether the traits that lead to take-over of a community

must be novel to the community or rather continuous traits that have extreme ("discrete") trait values (Chapin et al. 1996). Both strategies lead to successful invasion. For example, invasive plants were found to be on average taller than naturalized or native plants in temperate plant communities (Divíšek et al. 2018). Yet novel traits can allow introduced species to exploit a currently unoccupied niche by deploying a novel weapon (Callaway and Ridenour 2004).

The concept of EoTS can be applied across trophic levels. When plants are tightly coevolved with their microbial community, and if we consider these tightly coevolved relationships as an extended phenotype of a plant (Whitham et al. 2006), then one can widen the interpretation to be that the loss of the tightly coupled soil microbial symbionts—whether positive (like mycorrhizae) or negative (like pathogens)—can result in an introduced species being at the EoTS in its new range while the native species that have coevolved with their microbial community remains at the center of the functional trait space. If we assume that herbivores evolved with their plants in the native range, selection for reduced defensive compounds in the new range can allow plants to redeploy resources toward growth resulting in these newly evolved plants to be at the EoTS in their new community (Blossey and Notzold 1995).

Importantly, the conceptualization of optimal differentiation to EoTS does not focus on single traits but rather a multi-dimensional trait space; it is the combined trait profile of the introduced species and the native community that must be evaluated.

While EoTS does not have a direct analog for either phylogenetic or genomic "traits", patterns and processes manifest in these other dimensions of biological organization can shape the propensity of a species to be at the EoTS. As Darwin noted, phylogenetic distance from existing community members can provide a proxy for predicting the functional trait profiles in relation to EoTS of invaded communities since closely related species are more likely to have similar functional trait profiles. Yet, while ecosystem and phylogenetic processes define the constellation of resident species in the trait space, an introduced species can reorganize its genome by mixing widely divergent genomes, either between species (hybridization) or within species (admixture), and produce the underlying trait variation on which selection can operate to produce phenotypes that are at the EoTS of the recipient community (Fig. 1c). Genetic processes such as admixture and hybridization create, through transgressive segregation and recombination, genotypes with novel functional trait profiles that may be more likely to be at the edge of the community trait space. In the following we elaborate on how phylogenetics and genetics can further elucidate the concept of EoTS that is largely operating in the space of functional traits.

Phylogenetics and the EoTS

Traits evolve mostly in response to environmental conditions and thus vary across geography and among evolutionary lineages (Darwin 1859). Therefore, species' traits are not statistically independent from their shared evolutionary histories; this results in associations between the evolutionary relatedness of organisms in a community, their degree of similarity in functional traits, and the ecological processes that determine their distributions and abundance (Felsenstein 1985). Though trait expression can vary across space and time because of both genetic differences and environmentally induced phenotypic plasticity, often the key features expressed are constrained by phylogenetic inertia. While several studies have applied phylogenetic data to predict the success of introduced species, there does not appear to be a clear consensus in this regard—studies have shown that the

relationship between relatedness and the establishment success of introduced species can be positive, negative, or non-existent (Park and Potter 2013; Ng et al. 2019). Moreover, these studies do not differentiate between naturalized species (non-native but not dominant in the community; Richardson et al. 2000) and invasive ones (non-native and dominant in the community). Nonetheless, to the extent that the traits that influence community assembly are phylogenetically conserved, we may expect that the patterns that exist among native and invasive species in trait space will be reflected in phylogenetic space. Thus, if traits are phylogenetically conserved, we should see the patterns in measured trait distance between native and invasive species reflected in the phylogenetic tree—with species that are closer on the phylogenetic tree being more likely to be naturalized while those further away are more likely to be invasive (Fig. 1b). In other words, if successful invaders exist at the EoTS where they are neither too different nor too similar to native species in the community, they may also exist at the edge of phylogenetic space.

Part of the ambiguity surrounding the relationship between phylogenetic relatedness and invasion success may thus lie with the fact that successful invaders are phylogenetically 'just distant enough' from the native community, and the signal of optimal (phylogenetic) differentiation can be interpreted both ways depending on the scale of the study (Park et al. 2020). The lack of a metric to assess the relative distance between native community members and potential invaders creates this ambiguity. Calculations of the weighted phylogenetic distance of the native community to the phylogenetic distance for the introduced species would provide a clear signal as to whether the EoTS pattern applies to phylogenetic distances. A few recent phylogenetic studies suggest that EoTS may pertain. In an experimental study on grassland communities, Malecore et al. (2019) found that the successful invaders were neither too close nor too far with the optimal phylogenetic relatedness at an intermediate level of relatedness. Miller et al. (2017) compared the positions of non-introduced, introduced, naturalized and invasive species in the network derived from phylogenetic distances between species pairs, for the phylogenetic genera *Acacia* and *Eucalyptus.* They found that the more invasive *Acacia* species are located in a more marginal position in the phylogenetic network, whereas the less invasive *Eucalyptus* species reside more centrally located within the phylogenetic network.

Applying phylogenetic distance has the added benefit of encapsulating the entirety of species' characteristics underlying their evolutionary histories, as opposed to being limited to easily measured traits and/or traits present in online trait databases. However, genes and traits evolve at different rates and do not all follow the same evolutionary history within lineages; thus, phylogenetic patterns may not always prove informative in the context of community assembly (Park et al. 2020). Nonetheless, acquiring phylogenetic information has become easier due to advances in high-throughput sequencing and computation, and is less context-dependent than trait data, which are costly and time-consuming to collect. It should be straightforward to construct molecular phylogenies to elucidate relatedness between native and introduced taxa to identify the degree of phylogenetic differentiation between successful invaders and the native community and to repeat the EoTS analysis on the phylogenetic data.

Genomics and the EoTS

Genomics can provide an underlying mechanism for understanding how invasiveness may emerge as a result of the rapid evolution of traits towards the EoTS (Fig. 1c). Hybridization and polyploidization have been proposed as an evolutionary stimulus for biological

invasions (Ellstrand and Schierenbeck 2000; te Beest et al 2012; Hovick and Whitney. 2014), both at the inter-specific level as well as at the intra-specific level of admixture between divergent populations of the same species (Lavergne and Molofsky 2007; Keller and Taylor 2008). Indeed, many of the most highly invasive plants have a history of hybridization or genetic admixture (Ellstrand and Schierenbeck 2000), but the causative link between polyploidization, hybridization/admixture (hereafter referred to simply as "admixture"), and invasiveness is often left untested (but see Palacio-Lopez and Molofsky 2021). Admixture offers opportunities for recombination and the reorganization of the genetic architecture of functional traits, which can release phenotypic variation latent within species or populations that are not admixed. In some cases, this results in transgressive segregation; that is, the expansion of functional trait variation or multi-trait covariation due to the complementary action of alleles specific to each parental lineage that are recombined in hybrids (Rieseberg et al. 1999). Transgressive segregation following admixture is hypothesized to underlie the genetic architecture leading to adaptive radiation into new ecological niches (e.g., Lexer et al. 2003). Additionally, recombination during admixture can break up multi-trait correlations that may exist at the species or population level due to historic selection patterns on suites of traits (i.e., "selective covariance, Armbruster and Schwaegerle 1996). Both transgressive segregation and the breakup of selective covariance can result in the occupancy of new single or multi-trait space by recently admixed genotypes and may enable genotypes to move toward the EoTS in their recipient communities.

As in the community ecology context, there may exist an optimal degree of genetic differentiation whereby admixture is likely to come with benefits of expanding trait variance and evolutionary potential without reducing fitness. Mating between individuals whose genomes have diverged too much can result in reduced offspring fitness (outbreeding depression), while mating between individuals with minimally diverged genomes is less likely to result in novel genetic architectures (Lynch 1991). Thus, combining genomes through admixture that exhibit an intermediate level of divergence can result in individuals with extreme trait values and/or novel trait combinations, while avoiding outbreeding depression. This admixture between divergent genomes can provide a substrate for evolutionary change and may be responsible for the high number of successful invasive species post introduction. While hybridization and admixture are often studied during invasion, to our knowledge the idea that transgressive segregation leads to trait variation that is selected to occupy empty functional trait space remains untested.

Conclusion

Conflicting results about what mechanisms allow species to invade communities may be attributable to several opposing processes occurring over different scales of biological organization. The EoTS hypothesis resolves these issues by positing that species must be optimally differentiated from the resident community to invade. Further, the EoTS hypothesis provides testable hypotheses across the scales of biodiversity. It allows one to calculate a metric that provides a way to compare among diverse communities, phylogenies and genomes. With the advent of online databases, the concept of EoTS could be tested for functional traits, phylogenetic relatedness and genetic processes (Kattge et al. 2020). Moreover, the EoTS concept provides a mechanism whereby introduced species could acquire more extreme trait values necessary for community dominance and suggest which phylogenetic clades should contain species that are likely contenders. As we have imported the

concept of *optimal differentiation* from other disciplines, we suggest that other fields could adopt the concept of EoTS. The EoTS concept allows one to predict the degree of differentiation necessary for an entity to become successful. Thus, we propose the EoTS can be applied across other disciplines providing a measurable quantity that predicts when a new entity takes over an existing one.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Consent for publication The authors have consented to publication of this manuscript.

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