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PERSPECTIVES AND PARADIGMS

Can macroevolution inform contemporary invasion potential?

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Abstract The early identification of future invasive species is crucial for efficient management and preventing further biodiversity decline. Some general predictors of species' invasiveness, such as association with humans, propagule pressure and particular species' characteristics, are well established. However, obtaining these predictors can be costly and time-consuming, with varying predictive power across taxonomic groups and geographic contexts. To find general predictors of species' invasion potential that are straightforward to collect for large groups of species, a recent idea suggests the use of macroevolutionary indicators, such as diversification, niche evolution and past dispersal rates. These macroevolutionary rates are proposed as proxies for characteristics linked to invasion potential, such as ecological niche breadth, evolutionary capacity, or competitive ability. However, this assumption is rarely tested, which is why it is uncertain whether macroevolutionary indicators can serve as reliable predictors of invasion success. Here, we first identify the assumptions made in studies that link macroevolutionary rates to current invasions. Second, we review the literature to evaluate which of these assumptions are supported by scientific evidence. Third, we test whether past biogeographic dispersal ability is a good proxy for current naturalisation success in 12 groups of tetrapods. We conclude that macroevolutionary indicators have substantial potential for predicting species' future invasiveness. However, assumptions about the relationships between macroevolutionary indicators and species' traits must be rigorously tested. Further, different invasion pathways (e.g. unintentional vs intentional transport and introduction) and geographical contexts (e.g. continents vs islands) may introduce variability in any general relationships.

Keywords Naturalisation · Diversification rate · Biogeographic dispersal · Niche evolution rate · Speciation · Historical biogeography

Introduction

Biological invasions are one of the major causes of ecosystem declines and biodiversity loss, and the rate of establishment of non-native species is

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growing, indicating little success in preventive measures (IPBES 2019; Seebens et al. 2017). Prevention and management shortly after introduction is most efficient and effective (Simberloff et al. 2013). However, early identification of species with high invasion potential has been a long-standing problem (Fournier et al. 2019; Safriel and Ritte 1980; Theoharides and Dukes 2007).

To become invasive, species must overcome a series of barriers, and several factors are known to predict their success (Blackburn et al. 2011). First, species need to be transported from their native region and introduced elsewhere, which is more likely to happen, both unintentionally and intentionally, to species that have a strong association with humans (e.g. through pet trade, Lockwood et al. 2019; Street et al. 2023; Theoharides and Dukes 2007). Second, introduced species need to establish viable populations outside their native range for which they need to overcome survival and reproductive barriers. This is more likely for generalist and large-ranged species as they are more likely to find suitable habitat outside of their native range, and for species with a fast life history strategy and good competitive ability (Allen et al. 2017; Capellini et al. 2015; Hayes and Barry 2008; Pili et al. 2024; Rejmánek et al. 2005; Sol et al. 2012; Theoharides and Dukes 2007). In addition, a species frequently introduced in large numbers has a higher probability of establishment as high propagule size (many individuals introduced at once) lessens effects of demographic stochasticity and genetic bottlenecks, and propagule number (frequency of introduction events) diminishes the impacts of environmental stochasticity (Blackburn et al. 2015; Hayes and Barry 2008; Simberloff 2009). Third, established species need to overcome biotic and landscape barriers to spread from the founding population in order to become invasive. High propagule pressure (the combination of propagule size and number) makes success in this stage more likely, giving an advantage to fecund species with good dispersal abilities (Allen et al. 2017; Capellini et al. 2015). In addition, good competitive ability and high evolutionary potential will allow species to colonise more easily a diversity of novel environments (Pyšek et al. 2009; Theoharides and Dukes 2007; Vermeij 2005).

Despite these general relationships, many exceptions exist and predictors often vary across taxonomic groups and with biogeographic context, making it difficult to generate global predictions of species' invasiveness (Hayes and Barry 2008; Kueffer et al. 2013; Pili et al. 2020; Seebens et al. 2019). For instance, fast life histories promote invasion success in mammals, reptiles and amphibians while birds seem to profit more from a bet-hedging strategy (Allen et al. 2017; Capellini et al. 2015; Condamine et al. 2018; Sol et al. 2012). Further, the mechanisms of success can be related to different traits in different species. The success of the Russian olive (*Elaeagnus angustifolia*) invasion has been attributed to its dispersal ability and broad habitat suitability (Collette and Pither 2015; Courtney et al. 2024), whereas the success of the garlic mustard (*Alliaria petiolata*) invasion has been attributed to its production of allelochemical compounds providing a competitive advantage (Callaway et al. 2008). Lastly, different non-native populations of the same invasive species rarely perform in a similar way—a species might become very abundant in one region, but stay rare in another (Kueffer et al. 2013). This variability is partly attributable to regional effects mediated by abiotic and biotic conditions of the recipient community (Sax et al. 2005). Our ability to predict species' invasion success is thus inhibited by the fact that relationships between specific traits and invasion success differ from taxon to taxon, and that different underlying mechanisms, not always mediated by the same traits, can be responsible for success. Other species' characteristics that could potentially serve as reliable predictors, such as evolutionary potential or dispersal ability, are difficult and costly to measure and data are currently insufficient for practical use (Forsman 2014; Marin et al. 2020). Predicting species' invasion success therefore remains challenging (Gallien and Carboni 2017).

To find general predictors of species' invasion potential (here defined as species' potential to successfully naturalise), recent studies have turned towards macroevolutionary indicators, such as diversification rates or past biogeographic dispersal capacities, as these are straightforward to obtain for large groups of species and not limited to a single mechanism or trait (Gallien et al. 2019; Lenzner et al. 2020; Schmidt et al. 2021). Evolutionary rates and biogeographic movements measured over macroevolutionary timescales may reflect processes that happen during establishment and spread of contemporary invasions, such as trait or niche evolution and dispersal. Assuming that species' characteristics related to these processes are heritable, macroevolutionary indicators could thus be useful proxies for species' contemporary population and range dynamics (Fritz et al. 2013; Pimiento and Antonelli 2022). For instance, a fast rate of niche evolution could indicate that extant species are more prone to becoming invasive, as they should hold high capacities to adapt to new environmental conditions (Gallien et al. 2019). Extant descendants of a lineage that has made many biogeographic movements to successfully colonise distant locations in the past may be at higher risk of becoming invasive than descendants of a lineage with very few colonisations, as they may have inherited the good dispersal and establishment capacities of their ancestors (Gallien et al. 2016).

The proposal that macroevolution and historical biogeography can inform contemporary ecological dynamics is appealing, but also raises a number of concerns. In particular, the proposed link between macroevolutionary indicators and present-day invasion risk is based on the assumption that these indicators are proxies for characteristics linked to invasion potential (e.g. competitive ability, fast life history strategy, evolutionary potential). However, this underlying assumption is rarely directly tested. It is now time to critically evaluate the validity of the hypotheses linking macroevolutionary indicators to species' traits that facilitate contemporary invasions, in order to determine whether these indicators can be reliably used to predict invasion potential.

Here, we investigate whether macroevolutionary and historical biogeographic studies can help predict species' probability of invasion, and if so, under what conditions. We begin by describing the assumptions made in studies that link macroevolutionary indicators (rates of diversification, niche evolution and past dispersal) to current invasions. Then we review the literature to evaluate whether these assumptions are supported by evidence. To complement our findings regarding the link between past dispersal rates and current invasion success, which are currently restricted to three plant clades, we test this relationship quantitatively in 12 groups of tetrapods. Our results suggest that macroevolutionary indicators hold significant promise for predicting species' naturalisation potential, while also highlighting the challenges associated with their application.

Diversification rates as proxy for current invasion potential

Are lineages with high diversification rates—i.e. those with higher speciation than extinction rates—more or less likely to become invasive? Two opposing hypotheses have been put forward (Lenzner et al. 2020): (H1) Fast diversifying clades give rise to specialised, small-ranged endemics. Species with these characteristics are expected to perform poorly in biological invasions because of narrow ecological requirements and associated reduced colonisation potential. (H2) High diversification rates are indicative of high evolutionary potential ("the capacity to evolve genetically based changes that increase fitness under changing conditions", Forester et al. 2022) which is expected to be advantageous in biological invasions because it facilitates establishment and spread in novel regions through adaptation. In the following, we explain the reasoning behind these underlying assumptions, and review the literature to determine whether empirical evidence supports them (Fig. 1).

The evidence for underlying assumptions

Hypothesis 1—high diversification leads to low invasiveness—has two underlying assumptions: high diversification rates give rise to species that are (i) specialised, and (ii) small-ranged. Indeed, in various taxonomic groups, specialists tend to have higher diversification rates than generalists (Cantalapiedra et al. 2011; Gamboa et al. 2022; Hardy and Otto 2014; Menéndez et al. 2021; Rolland and Salamin 2016). Although large-ranged generalists may exhibit high diversification rates, for example after an interruption in gene flow following the appearance of geographical barriers, descendant species will generally occupy narrower adaptive spaces than parent species (Castiglione et al. 2017; Rolland and Salamin 2016; Sexton et al. 2017). This supports the first assumption of hypothesis 1 that fast diversifying clades lead to specialised species.

Regarding the relationship between diversification rate and range size, studies draw different conclusions. Some found that lineages with higher diversification rates tend to host extant species with narrower ranges (Greenberg et al. 2021; Greenberg and Mooers 2017; Leão et al. 2020), while others found opposite trends (Cardillo et al. 2003; Colston et al. 2020;

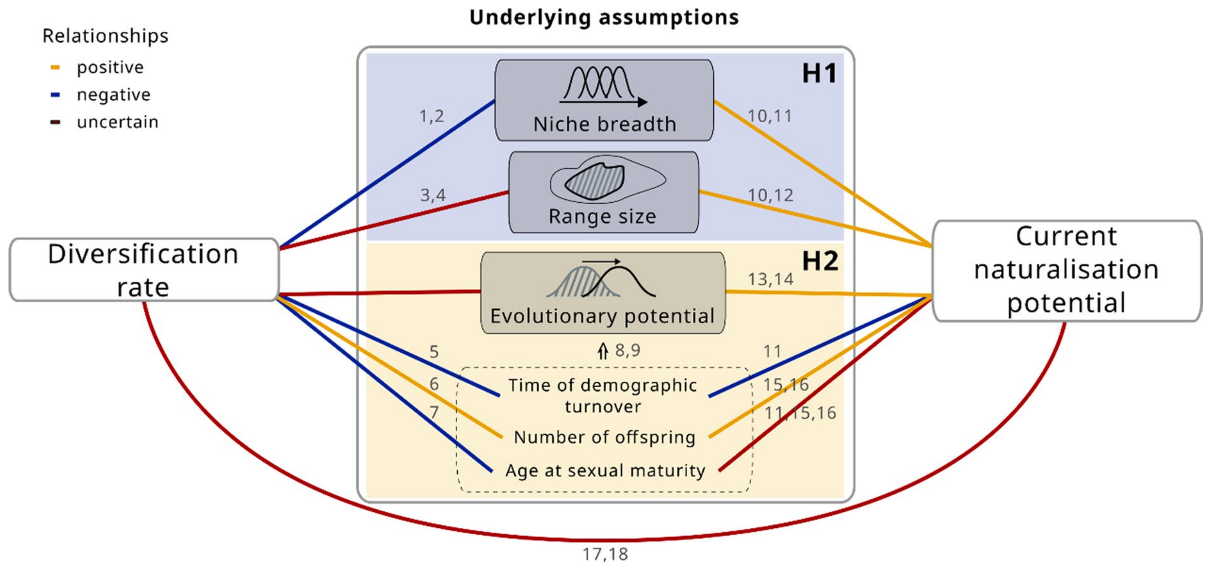


Fig. 1 Scientific support for the assumptions underlying the relationship between diversification rate and current naturalisation potential. Blue lines indicate negative relationships, yellow lines positive relationships and red lines uncertain relationships either due to insufficient investigation or due to contradictory studies. Empirical support is indicated by representative references: 1: Rolland & Salamin (2016), 2: Gamboa et al. (2022), 3: Greenberg et al. (2021), 4: Colston et al. (2020), 5: Baker et al. (2014), 6: Cardillo et al. (2003), 7: Verdú (2002), 8: Thomas et al. (2010), 9: Smith and Donoghue (2008), 10: Pili et al. (2024), 11: Theoharides and Dukes (2007), 12: Rejmánek et al. (2005), 13: Forsman (2014), 14: Pili et al. (2020), 15: Allen et al. (2017), 16: Capellini et al. (2015), 17: Lenzner et al. (2020), 18: Schmidt et al. (2021)

Redding et al. 2010; Ye et al. 2024). One explanation for these opposite findings may be that many studies have based their conclusions on correlations between current range sizes and tip estimates of diversification rates. A recent study used process-based models instead to investigate the effect of range size on diversification rate in mammals, accounting for cladogenetic changes in range size (Smyčka et al. 2023). They found that large-ranged species had higher diversification rates, likely because large ranges increase the variability of environmental conditions a species encounters, increasing opportunities for local adaptations. Additionally, these species were more likely to produce at least one small-ranged daughter species (see also Castiglione et al. 2017; Smyčka et al. 2023). However, in several clades small-ranged species diversified faster than large-ranged ones; often these were radiations in oceanic or continental island settings (Smyčka et al. 2023). Thus, although the process is the same in most clades (large-ranged species diversify faster and are likely to produce small-ranged daughter species), correlative approaches uncover a variety of different relationships. This is due to post-speciation changes in range size, i.e. the way and speed with which species' ranges change after speciation, which can vary substantially between and within clades (Miller 1997; Taylor and Gotelli 1994; Webb and Gaston 2000; Willis 1922).

Overall, the two assumptions underlying Hypothesis 1 are partly supported: while high diversification rates tend to be linked to current specialisation, this does not necessarily mean small range size. Range size is not directly mechanistically linked to invasion success; instead, it is used as a proxy for a number of traits that are known to increase invasion success. For instance, large-ranged species are more likely to come into contact with humans which increases the probability of human-mediated voluntary or involuntary transport and introduction elsewhere (Guo et al. 2024). Large-ranged species also generally have wider niches which facilitates naturalisation in varying environments, and are generally better dispersers than small-ranged species, although the relationship between range size and dispersal ability has been shown to be clade-dependent (Alzate and Onstein 2022; Lester et al. 2007; Slatyer et al. 2013). While species descended from lineages with high diversification rates might thus be generally more specialised, this is not sufficient to conclude likely low invasion potential if the underlying assumption regarding the link between diversification rate and range size (or other direct traits associated with invasion, such as dispersal ability) has not been explicitly tested.

Hypothesis 2—high diversification leads to high invasiveness—has one underlying assumption: high diversification rates are indicative of species with high evolutionary potential. Most empirical support for this assumption is indirect because evolutionary potential is difficult to measure directly. Instead, certain traits and population characteristics, such as generation time, have been used as a proxy for evolutionary potential (Smith and Donoghue 2008; Thomas et al. 2010). High diversification rates have been linked to short generation times, measured by age at maturity (in woody angiosperms: Verdú 2002), and demographic turnover times (in Amazonian trees: Baker et al. 2014), as well as high population growth rates, measured by litter size (in Australian mammals: Cardillo et al. 2003), or body size (in South African stone plants: Boucher et al. 2017; in actinopterygian fishes: Tedesco et al. 2017). These characteristics are generally beneficial in the colonisation of new habitats (Allen et al. 2017; Capellini et al. 2015; but see Sol et al. 2012): on the one hand, species with these characteristics can adapt more easily to new conditions. On the other hand, high population growth rates reduce the period of low population size at the beginning of colonisation, resulting in decreased risk of stochastic extinction of the founder population. Therefore, there is indirect empirical support for the validity of Hypothesis 2.

Linking past and present

Two recent studies investigated the direct link between diversification rates and contemporary naturalisation potential. Schmidt et al. (2021) found a negative relationship between diversification rates and naturalisation success in angiosperm families, indicating that descendants from fast diversifying clades are likely to be poor invaders (i.e. support for Hypothesis 1). In contrast to this, Lenzner et al. (2020) found a positive relationship between diversification rates and naturalisation success (i.e. support for Hypothesis 2). The two studies quantified naturalisation success slightly differently: Schmidt et al. (2021) used the proportion of naturalised species per family whereas Lenzner et al. (2020) multiplied this variable with the number of regions where each species was naturalised. These seemingly opposite results thus indicate that species with high diversification rates are less likely to establish populations elsewhere (Schmidt et al. 2021), but those that do are likely to be disproportionately successful and establish in many regions (Lenzner et al. 2020, Box 1, Fig. 2).

Box 1 How do diversification rates influence current naturalisation potential?

Two recent studies found opposite relationships between diversification rates and current naturalisation success in angiosperm families (Lenzner et al. 2020; Schmidt et al. 2021). Naturalisation success was quantified either as the proportion of naturalised species per family (Schmidt et al. 2021; included 395 families, result: negative relationship) or as the proportion of naturalised species per family multiplied with the number of regions where each species was naturalised (Lenzner et al. 2020; included 168 families, result: positive relationship; for simplicity we refer to this definition henceforth as naturalisation success). The seemingly opposite results can be reconciled if species with high diversification rates rarely establish elsewhere, but those that do establish in many regions. We investigated this hypothesis in a unified statistical framework. To do so, we extracted all relevant data from Lenzner et al. (2020): family-level diversification rates, naturalised and total species richness per family, and naturalisation success. From this data we also calculated the proportion of naturalised species per family. Then we tested if diversification rates jointly influenced naturalisation success and proportion of naturalised species per family, with a multivariate multiple regression. To do so we used the lm function in R (version 4.3.2, R Core Team 2023) and a type II ANOVA (Anova function from the R package "car", Fox and Weisberg 2018), on log-transformed and scaled variables. This overall model was statistically significant (Pillai's trace $=0.51$, $F(2, 119)=61.41$, p-val <0.001), and supported our hypothesis. As in the previous studies, diversification rate was negatively related to

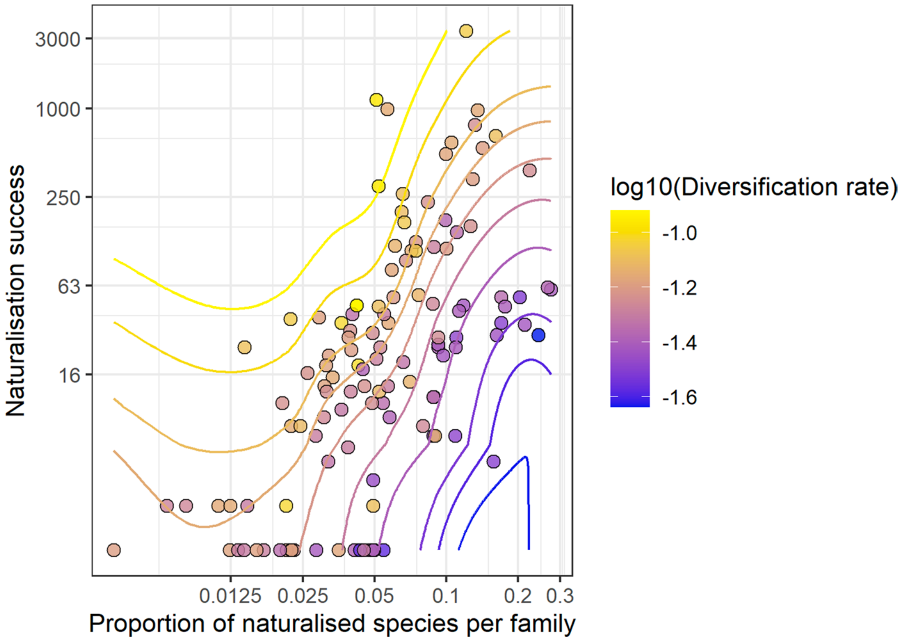


Fig. 2 Relationship between the proportion of naturalised species per family, naturalisation success, and diversification rates based on data from Lenzner et al. (2020). Naturalisation success is quantified as the proportion of naturalised species per family multiplied with the number of regions where each species was naturalised. Diversification rates are indicated by the colour gradient and by contour lines. Variables are presented on a log10 scale for visualisation purposes. Only families with at least one invasive species and with data on naturalisation success were included (n = 122).

the proportion of naturalised species per family (coef = – 0.32, standard error = 0.09, *p*-val < 0.001, Fig. S1a) and positively to naturalisation success (coef = 0.30, standard error = 0.09, *p*-val < 0.001, Fig. S1b). This indicates that families with high diversification rates (yellow colours, Fig. 2) tend to have a lower proportion of naturalised species but greater naturalization success (i.e. they establish in more regions).

Following our investigation of the hypotheses and assumptions linking diversification rates to contemporary invasion potential we can attempt to explain the processes behind these findings. We found that species descended from lineages with high diversification rates tend to be specialised, but that their ranges can be either small or large depending on post-speciation range changes. While specialised species with small ranges likely have low overlap with humans and little opportunity to move or be moved elsewhere, those species that do expand their ranges after speciation might have specific advantages in invasions. First, their ranges are large, so they have increased opportunities for transport and introduction. Second, they already proved able to expand their range after speciation which might be linked to traits that are also advantageous in invasions, such as good dispersal ability. Third, species descended from lineages with high diversification rates are likely to have good evolutionary potential (see investigation of the underlying assumptions of hypothesis 2 above). Taken together, this indicates that high diversification rates alone might not be a good indicator of invasion success, but that the combination of large range size and high diversification rate could prove useful (Lenzner et al. 2020). It would be very valuable to complement Lenzner et al. (2020) and Schmidt et al. (2021)'s family-level studies with an investigation of this prediction at species level.

We found one fact in our analysis of underlying assumptions that seems counter to Lenzner et al. (2020)'s finding that naturalisation success was highest for species with high diversification rates: high diversification rates generally lead to specialised species, which generally have low invasion potential (e.g. Pyšek et al. 2009). However, species' niches are multidimensional (Carscadden et al. 2020; Emery et al. 2012; Sexton et al. 2017), and while a species may be a specialist in one dimension it may be a generalist in another (e.g. Litsios et al. 2014). To better understand which type of specialisation is likely to hinder or facilitate invasions and in which contexts (e.g. a narrow climatic niche might inhibit establishment of species introduced to temperate regions due to larger seasonal changes, but not necessarily to tropical regions), it would be interesting to test in which dimension, if any, successful invaders descended from lineages with high diversification rates are specialised (e.g. habitat, environmental tolerances, plant-pollinator interactions).

Past rates of niche evolution as proxy for current invasion potential

High evolutionary potential is an advantage in contemporary invasions, particularly in the stages of establishment and spread, because it allows species to rapidly adapt to novel environmental conditions encountered in a novel region and can lead to the selection of genotypes with high colonisation abilities (Forsman 2014; Lavergne and Molofsky 2007; Phillips et al. 2010). However, evolutionary potential is challenging to quantify (Forester et al. 2022) which inhibits its use as a predictor of species' invasion potential. A possible solution is to use niche evolution rates, estimated from species-level phylogenies and extant species' niches, which are proposed proxies of evolutionary potential (Gudde and Venditti 2016; Salamin et al. 2010).

The evidence for underlying assumptions

The assumptions underlying the direct link between past rates of niche evolution and contemporary invasion potential are that (i) high niche evolution rates are correlated with high evolutionary potential, and that (ii) high evolutionary potential increases invasion success (Fig. 3). Species descended from lineages with high niche evolution rates would thus be expected to have high invasion potential (Gallien et al. 2016).

We found only a single study testing explicitly assumption 1, and its results supported the assumption. By comparing contemporary and fossil datasets, Holstad et al. (2024) showed that trait divergence correlates positively with evolvability at population and species level (measured as within-population mean-scaled additive genetic variance in the present and mean-scaled within-sample phenotypic variance in the past).

There is also support for the second assumption: higher levels of genotypic and phenotypic diversity (often used as proxies for evolutionary potential, Forester et al. 2022; but see Holderegger et al. 2006), generally increase establishment success of introduced species (Forsman 2014). The high adaptability of invasive species has been described as a paradox since they often have small founder population and hence limited genetic variability, which should limit their evolutionary potential (Allendorf and Lundquist 2003; Carneiro and Lyko 2020; Chown et al. 2015). However, in many cases, no real genetic paradox exists with invasive populations having as much or more genetic variance compared to their native counterparts due to large numbers of introduced individuals or repeated introductions (Bossdorf et al. 2005; Estoup et al. 2016; Lavergne and Molofsky 2007). In other cases, species have spread successfully from introduced populations with low genetic

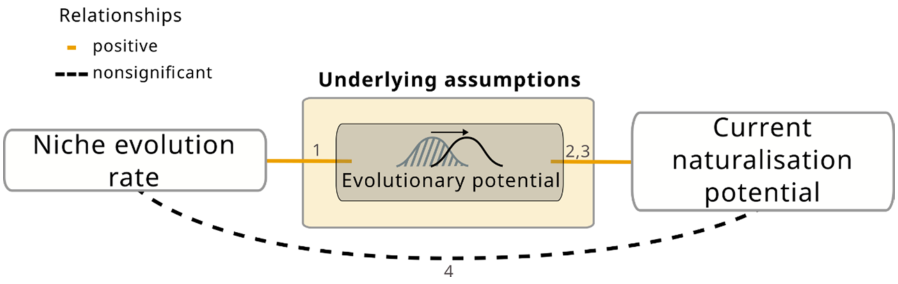


Fig. 3 Evaluating scientific support for the assumptions underlying the relationship between diversification rate and current naturalisation potential. Yellow lines indicate positive relationships and the black dashed line a non-significant relationship. Empirical support is indicated by representative references: 1: Holstad et al. (2024), 2: Forsman (2014), 3: Pili et al. (2020), 4: Gallien et al. (2016)

diversity (Darling et al. 2008; Myburgh et al. 2007; Richards et al. 2012). This has been linked to high phenotypic diversity despite only moderate or low genetic diversity (Vignon et al. 2023). Other factors include the nature of the invaded environment, genetic bottlenecks increasing population fitness by having positive effects on invasion-relevant traits, or sufficient appearance of new mutations to restore evolutionary potential (Chown et al. 2015; Estoup et al. 2016; Moran and Alexander 2014). Altogether, there are numerous examples of invasive species evolving rapidly after introduction (Atwater and Barney 2021; Fetters and Mcglothlin 2017; Gallien et al. 2016; Hudson et al. 2016; Pili et al. 2020; Whitney and Gabler 2008; Wiens et al. 2019, but see Liu et al. 2020). However, there are exceptions to this: in plants in particular clonality and self-compatibility have also been shown to be advantageous in invasions because they allow rapid growth after introduction, leading to high local abundance and spread rates (Catford et al. 2016; Hollingsworth and Bailey 2000; Loomis and Fishman 2009).

Linking past and present

Despite theory linking niche evolution rates to species adaptability and contemporary invasion potential, empirical tests showed non-significant results in pine tree invasions (Gallien et al. 2016). However, to our knowledge, this is the only study directly exploring the link between niche evolution rates and contemporary invasion potential—more investigation in this direction seems promising.

In this context, an important question lies in the niche dimension or biological trait whose adaptability may be important to invasion. The importance of various niche dimensions may vary depending on the specific alien species or the characteristics of their introduced ranges. For instance, naturalisation and spread might not only be promoted by evolution of the climatic niche (as assumed in Gallien et al. 2016) but can also be promoted by evolution of a more dispersal-prone phenotype by changing morphology (cane toads in Australia: Phillips et al. 2010), or adaptation to new feeding resources (soapberry bugs: Carroll et al. 2001).

Past biogeographic movements as proxy for current invasion potential

Successful biogeographic movements in the history of clades that led to lineages crossing barriers and colonising new areas may be related to the ability of their extant descendants to establish in new environments. This is because successful dispersal and establishment in the past (historical biogeographic movements) and today (human-mediated invasion) may depend on the same traits that extant species may have inherited (Gallien et al. 2016).

The evidence for underlying assumptions

Three assumptions underlie the link between past biogeographic movements and contemporary naturalisation potential which we investigate in the following section: (i) species' biogeographic movements can be explained by certain biological traits, (ii) these traits are highly heritable and show phylogenetic signal (i.e. closely related species are likely to share similar traits), and (iii) the same traits that facilitated past biogeographic dispersal also facilitate contemporary invasion.

The first assumption that species' traits influence successful dispersal across major biogeographic barriers and establishment in new biogeographic regions has recently accumulated evidence. That species differ in their dispersal and establishment abilities has been known for a long time, but dispersal across major biogeographic barriers has often been thought to be mainly determined by chance (Lowe and McPeek 2014; Nathan 2001; Simpson 1940). However, investigations of assemblages on oceanic islands revealed that species that succeeded in colonising these places often had distinct traits (Carlquist 1966; Schrader et al. 2024). Recently, process-based macroevolutionary models have supported these findings, showing for instance that Podocarpaceae species with fleshy cones, indicating predominance of animal dispersal, have a higher rate of dispersing successfully across long distances (Klaus and Matzke 2020). In addition, body size and life history strategy have influenced past biogeographic dispersal success in different ways in tetrapod clades (Nicolaï and Matzke 2019; Weil et al. 2022, 2023).

The second assumption, that traits related to dispersal and establishment are highly heritable and exhibit strong phylogenetic signal, is generally supported by the literature; however, the magnitude of heritability and phylogenetic signal varies among taxa and trait types. Meta-analyses indicate that heritability estimates for body size traits are typically higher than for life history traits (mean narrow-sense heritability $h^2_{\text{body size}} = 0.46 \pm 0.004$ (± standard error) compared to $h^2_{\text{life history}} = 0.26 \pm 0.012$; Mousseau and Roff 1987; see also Kingsolver et al. 2001; Réale et al. 2003). A similar pattern has been found for phylogenetic signal (mean Pagel's $\lambda_{\text{body size}} = 0.85 \pm 0.07$ compared to $\lambda_{\text{life history}} = 0.27 \pm 0.14$; Freckleton et al. 2002; see also Kamilar and Cooper 2013). These findings confirm that while all traits are heritable to some extent, the degree of heritability and phylogenetic signal can differ substantially across traits and clades.

For past dispersal rates to be a reliable predictor of invasion potential, the third underlying assumption is that the same traits need to be related to past biogeographic dispersal and present invasions. Traits that have been linked to past biogeographic dispersal success are similar to those that have been shown to facilitate success in biological invasions, including life history strategy and body size (Allen et al. 2017; Pili et al. 2024; Roy et al. 2002). However, while relationships between traits and past biogeographic dispersal capacities are clade-dependent (in tetrapods: Weil et al. 2023), relationships between traits and invasion success are more consistent (but still sometimes context-dependent and with exceptions, see Seebens et al. 2019). For instance, a fast life history strategy is generally advantageous due to its effects on population growth, facilitating establishment, and it has also been related to evolutionary potential, facilitating rapid adaptation to new conditions (Allen et al. 2017; Capellini et al. 2015; Smith and Donoghue 2008; Thomas et al. 2010, see also Sect. "Diversification rates as proxy for current invasion potential"). The link between body size and invasion success is more indirect; large bodied species generally have larger ranges than small-bodied species (Gaston and Blackburn 1996; Kolb et al. 2006; Mashau et al. 2021; Tucker et al. 2014), which makes it more likely for them to be associated with humans and transported (Guo et al. 2024), and increased dispersal potential has also been associated with large body size (Clobert 2012), which facilitates spread after successful establishment.

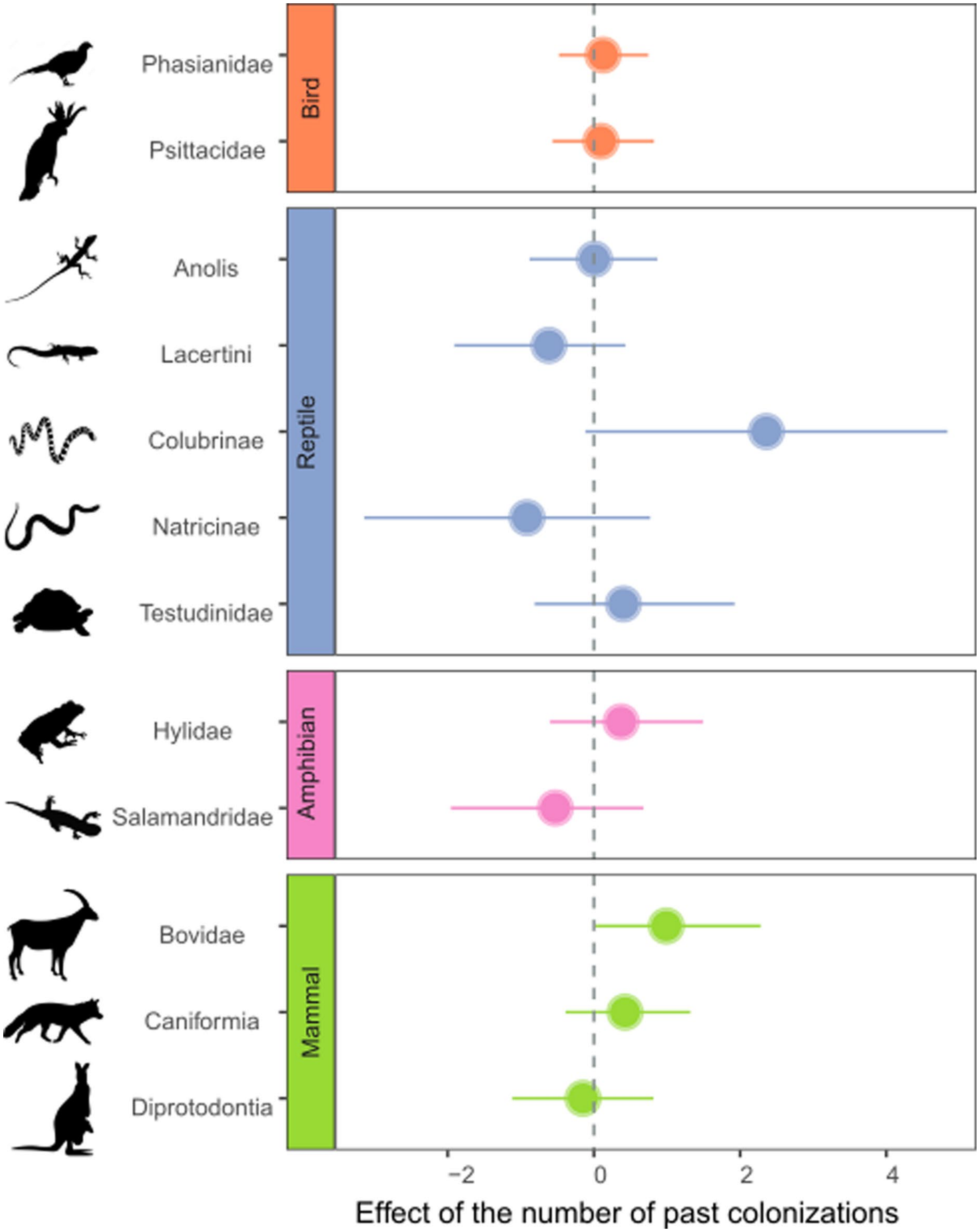
In summary, past dispersal rates can be expected to be a good proxy of current invasion potential if the relationships between traits and past dispersal success are the same as between traits and current invasion potential, and if heritability and phylogenetic signal of these traits are strong. However, relationships between traits and past dispersal are only just beginning to be formally investigated with process-based models. Initial results show that these relationships are clade-dependent, just like heritability and phylogenetic signal of traits, indicating that past biogeographical movements are only likely to be good proxies for invasion success in a subset of clades.

Linking past and present

The association of successful past dispersal and present-day naturalisation success has been confirmed for the genus *Pinus* (Gallien et al. 2016), as well as Australian acacias and eucalypts (*Acacia* sensu stricto and the clade *Angophora*, *Corymbia*, *Eucalyptus,* Gallien et al. 2019). To understand if these trends reflect a general rule across the tree of life, or whether they are specific to a few clades, we test this association in 12 clades of tetrapods (Box 2). We find that in those clades, the number of past biogeographical movements of a lineage does not significantly predict the naturalisation success of its descendants.

While there is evidence for a link between past biogeographic dispersal and current establishment in the context of biological invasions, there is a lot of uncertainty associated with the individual assumptions (e.g. clade-dependent relationships between traits and past dispersal success, varying strength of heritability and phylogenetic signal in those traits, context-dependent relationships between traits and current establishment success). In addition, biological invasions differ in multiple ways from past natural dispersal, in particular in the types of species that are transported and in the intensity that individuals are transported (Vermeij 2005).

It is curious that plant clades showed significant relationships between past biogeographic dispersal and success in current biological invasions while animal clades did not. These initial investigations are limited by sample size (amongst others, Box 2) and it would be interesting to test the relationship for additional taxa to understand if the division between animals and plants is a general one. In particular, some


Bird
Phasianidae
Psittacidae
Reptile
Anolis
Lacertini
Colubrinae
Natricinae
Testudinidae
Amphibian
Hylidae
Salamandridae
Mammal
Bovidae
Caniformia
Diprotodontia
−2
0
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4
Effect of the number of past colonizations

◀**Fig. 4** Test of the relationship between past colonisation rates and contemporary naturalisation success in 12 clades of tetrapods. The figure shows, for each clade, the standardised effect size of the number of past colonisations on naturalisation (dots), as well as 95% confidence intervals (horizontal bars), as determined through logistic regressions. The effect of past colonisations of current naturalisation success was non-significant in all clades. Icons: phylopic.org

clades that include well-known invaders such as rats or sparrows, would be an interesting addition.

Box 2 Is the number of past colonisations a good proxy for invasiveness?

We tested if species' past biogeographic dispersal success can be used as a proxy for their present-day naturalisation capacity in biological invasions. To do so, we combined biogeographic histories of tetrapod clades (Weil et al. 2023) with existing naturalisation data (Allen et al. 2017; Capellini et al. 2015; Sol et al. 2012). 12 of the 56 tetrapod clades treated in Weil et al. (2023) had sufficient naturalisation data for our purposes (Phasianiae, Psittacidae, Anolis, Lacertini, Colubrinae, Natricinae, Testudinidae, Hylidae, Salamandridae, Bovidae, Caniformia, Diprotodontia; Tab. S1). Weil et al. (2023) compiled and processed phylogenetic and species' distribution data from various sources to estimate clades' biogeographic histories, i.e. dispersal, vicariance and range contractions, between predefined discrete areas (phylogenies: Hugall and Stuart-Fox 2012; Jetz et al. 2012; Jetz and Pyron 2018; Thomson et al. 2021; Tonini et al. 2016; Upham et al. 2019; species distribution data: BirdLife International and Handbook of the Birds of the World 2019, IUCN 2019, and gbif.org,). We used their models as a base to generate 100 biogeographic stochastic maps per clade (BSMs, Dupin et al. 2017) and estimate species' past colonisations between biogeographic regions that were also defined at clade-level (see Weil et al. 2023 for details of the bioregions between which dispersal events were estimated). The number of colonisation events was counted as the number of dispersals between bioregions for each species' lineage averaged across all 100 BSMs. To be able to compare clades with each other, we standardised the number of past colonisations at clade level. Finally, we compared introduced and naturalised species with introduced but not naturalised species and tested if colonisation number was related to present-day naturalisation success using logistic regressions (if phylogenetic signal was present in the residuals, we used phylogenetic logistic regressions instead, R package "phylolm" v2.6.2, Ho and Ané 2014).

While previous work found a significant relationship between past colonisations and present-day naturalisation success in three plant clades (pines, eucalypts and acacias, Gallien et al. 2016, 2019), we did not find any significant relationships in tetrapod clades (Fig. 4). One possible explanation for this is that the pool of introduced species was already heavily biased in terms of introduction pathways (Allen et al. 2017; Capellini et al. 2015). Among the 12 tetrapod clades, 50% of species were introduced and released intentionally, and human activities, particularly pet trade, have been shown to favour species with certain traits (Street et al. 2023). In contrast to this, plants are more often transported unintentionally or escape involuntarily after intentional transport, rather than being released intentionally (Hulme et al. 2008). It is also possible that, for our clades of tetrapods, other factors not captured by lineages' past colonisation history are essential in naturalisation success, such as introduction effort (Allen et al. 2017; Capellini et al. 2015; Cassey et al. 2018). In particular, phenotypic and ecological diversity varies greatly among our clades, and traits other than dispersal are known to be influence invasion. Consequently, a joint analysis of past colonisation ability and other traits may offer a more comprehensive approach for future research.

Lastly, several methodological advances could improve this analysis. (1) We estimated the number of colonisations independently for each clade. However, to build invader black lists that cover and compare multiple clades, it would be better to fit biogeographic models on all clades simultaneously. Yet, doing so requires accounting for large numbers biogeographic regions (more than 9 in most cases), which is currently a challenge in terms of computational power, but also an interesting research avenue. (2) Additionally, increasing the number of bioregions would allow more detailed estimates of lineages' dispersal abilities within a single clade. This might allow a distinction between different types of dispersal, e.g. ecological versus biogeographic dispersal, and identify the relative importance of short-distance ecological compared with long-distance biogeographic events. (3) Finally, our dispersal estimates are based solely on the phylogenies of extant species, and could gain from the inclusion of dated fossils. Fossil data is an essential source of information that can be used to improve the estimates of lineages' past movements (potentially changing dispersal estimates in lineages; Coiro et al. 2023) and to validate lineages' past localities.

Conclusion

We show how three macroevolutionary indicators, namely diversification rates, niche evolution rates and past biogeographic dispersal rates, can be linked to contemporary biological invasion potential. We find empirical support for all implicit assumptions underlying the links between macroevolutionary indicators and invasion potential. However, the evidence is tentative or indirect for some assumptions, highlighting the necessity for more research, especially regarding the links between (i) diversification rates and range size, taking temporal evolution of range size into account, (ii) diversification rates and evolutionary potential, and (iii) niche evolution rates and evolutionary potential.

Regarding the direct links between macroevolutionary indicators and invasion potential, we find diversification rates can be linked to naturalisation potential at family level in plant clades. Future research should focus on species-level analyses to be relevant for management decisions. Analyses in additional taxonomic groups and analyses integrating diversification rates and range size could be promising. Niche evolution rates were poor proxies for species' evolutionary potential in pines, but the underlying assumptions are well supported by the literature, encouraging future studies in this direction. Next, while a positive association between past dispersal and naturalisation success had been found in three plant clades, we could not confirm this for 12 tetrapod clades. This indicates the need to test underlying assumptions for individual clades.

Altogether, we conclude that macroevolutionary indicators have substantial promise for predicting species' current invasion potential. If the underlying assumptions hold, these indicators can be calculated for large numbers of species with relatively little primary data (i.e. phylogenetic data). However, we urge scientists to be cautious when employing this approach. Some underlying assumptions regarding relationships between macroevolutionary indicators and species' traits cannot be taken for granted and need to be explicitly tested. Additionally, the complexity of invasions—in terms of the diversity of invasion pathways, the diversity of introduced species, and the diversity of recipient ecosystem—is likely to add significant noise to any general relationships (Kueffer et al. 2013; Novoa et al. 2020; Seebens et al. 2019). Since macroevolutionary indicators are calculated at broad temporal and spatial scales, species-level inferences may often be misleading, and exceptions to general relationships between macroevolutionary indicators and invasion potential are to be expected. Therefore, while macroevolutionary indicators offer a promising tool for predicting invasion potential, their application requires careful validation and consideration of the multifaceted nature of biological invasions.

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Author contributions LG and SSW devised the project and the main conceptual ideas; MH and SSW conducted the quantitative analyses; SSW conducted the literature review and wrote the original draft; LG, SL, and WLA reviewed and edited the manuscript; LG and WLA acquired funding. All authors read and approved the final manuscript.

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Data availability Data and code supporting the results of the reanalysis investigating the effect of diversification rate on naturalisation success, as well as the results of the analysis investigating the effect of past dispersal success on contemporary naturalisation success are available at https://doi.org/10.5281/zenodo.15504734.

Declarations

Conflict of interests The authors have no competing interests to declare that are relevant to the content of this article.

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