

Expanding the invasion toolbox: including stable isotope analysis in risk assessment

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Abstract

Species introductions are a major concern for ecosystem functioning, socio-economic wealth, and human well-being. Preventing introductions proved to be the most effective management strategy, and various tools such as species distribution models and risk assessment protocols have been developed or applied to this purpose. These approaches use information on a species to predict its potential invasiveness and impact in the case of its introduction into a new area. At the same time, much biodiversity has been lost due to multiple drivers. Ways to determine the potential for successful reintroductions of once native but now extinct species as well as assisted migrations are yet missing. Stable isotope analyses are commonly used to reconstruct a species' feeding ecology and trophic interactions within communities. Recently, this method has been used to predict potentially arising trophic interactions in the absence of the target species. Here we propose the implementation of stable isotope analysis as an approach for assessment schemes to increase the accuracy in predicting invader impacts as well as the success of reintroductions and assisted migrations. We review and discuss possibilities and limitations of this methods usage, suggesting promising and useful applications for scientists and managers.

Keywords

Impacts, mixing models, modelling, prediction, screening, stable isotope analysis

Introduction

Species introductions are an increasing concern for global biodiversity conservation (Doherty et al. 2016; Ricciardi et al. 2017; Bradley et al. 2019). This includes foremost the introduction of alien species, i.e. those species accidentally or intentionally moved outside their natural geographic range by humans, which shows no sign of saturation (Seebens et al. 2017). Introduced species often interact (Vesely et al. 2021), in many cases facilitating each other's establishment (Simberloff and Von Holle 1999), increasing their impacts due to interactions with anthropogenic stressors such as pollution (Crooks et al. 2011) and climate change (Hellmann et al. 2008; Rahel and Holden 2008; Beaury et al. 2020) and thereby become invasive. In addition to impacts on ecosystems (Ehrenfeld 2010), negative effects on human health (Mazza and Tricarico 2018) and ecosystem services (Walsh et al. 2016), as well as increasing economic costs due to direct damages (Ahmed et al. 2021a, b; Angulo et al. 2021) and associated management (Bradshaw et al. 2016; Diagne et al. 2021) are increasingly recognized.

To be effective, efforts to control invasive species should follow the hierarchical approach of the 2002 Convention on Biological Diversity, with prevention as the best option (Simberloff et al. 2013; Roy et al. 2019). For this purpose, risk screenings that identify which species should undergo a comprehensive risk assessment as well as standardized risk assessment protocols to identify potentially arising new threats have been developed (Essl et al. 2011; Vilizzi et al. 2021). These primarily aim at the identification of the most harmful species, pathways, and susceptible (invadable) sites whose protection should be prioritized (McGeoch et al. 2016). Risk assessments are usually designed for specific taxonomic groups (Copp et al. 2009; Brunel et al. 2010), vectors (Gollasch and Leppäkoski 2007), ecosystems (Leidenberger et al. 2015), or geographic regions (Baker et al. 2008), although more comprehensive protocols have been proposed (Copp et al. 2016; Davidson et al. 2017). Overall, these protocols attribute a total score summing the separate scores of assessments of species traits, ecological impacts, distribution, and control feasibility, for each of which an uncertainty level is provided (Dahlstrom et al. 2011; Srèbaliènè et al. 2019).

Together with predictive models, which use the ecological niche of an invasive species to probabilistically predict its future invaded range (Mainali et al. 2015; Uden et al. 2015), risk assessments are the main tools used to inform decision-makers and wildlife managers and provide fundamental information for legislations that prevent further invasions (Fournier et al. 2019), also in the context of future climate change scenarios (Chai et al. 2016). More recently, risk assessments and species distribution models have been used in combination, increasing the realism and accuracy of the predictions (Chapman et al. 2019; Yoğurtçuoğlu et al. 2021). Alternative taxa-specific approaches are trait-based models that scan a species list using ecological traits from known invasive species to identify potential new invaders (Howeth et al. 2016; Fournier et al. 2019). However, information is often missing, scarce, or anecdotal, particularly on impacts, leading to the assignment of “no potential impact” (Davidson and Hewitt 2014; Davidson et al. 2017) or “data deficient” (Kumschick et al. 2020).

On the other hand, species reintroductions, i.e. the translocation of individuals to areas in which a species became extinct with the aim of re-establishing a self-sustaining population, are of considerable value for conservation efforts (Haase and Pilotto 2019) but rarely successful – mostly due to life-cycle complexity or unpredictable external stressors (abiotic stress; biotic stress such as competition and predation; for a detailed account see Jourdan et al. 2019). Indeed, following the local extinction of a species, multiple factors can inhibit the occurrence of natural recolonization (Kail et al. 2012). For this reason, habitat restoration projects are often undertaken (Loch et al. 2020), although they too may fail due to various unforeseen factors (Bond and Lake 2003; Roni et al. 2018). Nevertheless, reintroductions are commonly used as a tool for wildlife rehabilitation (Armstrong and Seddon 2008), while the effectiveness of such reintroduction attempts themselves will depend on several intrinsic and extrinsic factors (Jourdan et al. 2019). Particularly, the interactions with other unwanted co-occurring species (i.e. alien species) can lead to failure of the reintroduction efforts (Cochran-Biederman et al. 2015).

Similar hurdles are faced by new conservation methods that have been proposed, like assisted migrations, i.e. the translocation of individuals to areas where they are predicted to move according to climate change but are not able to do so naturally (Hällfors et al. 2017). Some threatened species that could naturally move into new areas in accordance with their environmental and ecological requirements are inhibited to do so by limited time or human disturbances. For example, the presence of artificial barriers to natural dispersion can impede the ability of a species to respond to climate change and maintain its populations (Schwartz et al. 2012). Assisted migrations allow individuals to overstep such barriers in reasonable times to aid the species avoiding extinction (Schwartz et al. 2012). Although this approach has already been used (Willis et al. 2009), its application is still largely debated (Pérez et al. 2012; Schwartz et al. 2012) and depends on a trade-off between costs and benefits (Hoegh-Guldberg et al. 2008). For example, assisted migrations may lead to conservation paradoxes of species considered as endangered in their native range but recognized as invasive in their introduced range (Marchetti and Engstrom 2016; Marková et al. 2020). Accordingly, other criteria like feasibility of the translocation and collateral impacts (including the arising biotic interactions) need to be considered (Richardson et al. 2009; Hällfors et al. 2017). Therefore, the implementation of biotic outcomes prediction is crucial to assess whether assisted migration is an advantageous conservation strategy (Peterson and Bode 2021).

In all these cases – ranging from biological invasions to conservation biology – the arising biotic interactions, such as trophic relationships, are difficult to predict, while representing a crucial point for effective forecasting. In particular, what is still lacking is a fine-scale prediction of potential trophic impacts (in terms of predation and competition) on the recipient community and trophic pressures that focal species will encounter. Here we propose the use of stable isotope analysis as a tool for assessment schemes to predict such trophic relationships, and discuss the requirements, advantages, and assumptions of such an approach.

Stable isotope analysis (SIA)

General description

Stable isotope analysis (SIA) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) can reveal long-term and time-mediated information of a community's trophic structure and connectance (Boecklen et al. 2011; Layman et al. 2012; Middelburg 2014). Moreover, SIA can be used to quantify ecological niches, reveal trophic interactions as well as feeding preferences (Kelly 2000; Newsome et al. 2007), and enable the estimation of trophic levels (Post 2002; Quezada-Romegialli et al. 2018). Carbon signatures relate to the major energy sources, while nitrogen to the trophic position of a consumer within a food web (Fry 2006; Layman et al. 2012) due to predictable changes in the isotopic signal from prey to consumer, being enriched by 1‰ for carbon and by 2.5–5‰ for nitrogen between consecutive trophic levels (Post 2002; Vanderklift and Ponsard 2003). Using mixing models, it is also possible to determine the contributions of different prey items to the diet of a consumer (Phillips et al. 2014), with the possibility of including literature-based information or diet analysis data as priors to increase the analysis accuracy (Parnell et al. 2013).

Stable isotope analysis has been proven to be a useful tool in the field of invasion ecology (Vander Zanden et al. 1999). It is often used to assess the impacts of introduced species on other taxa in term of predation (Haubrock et al. 2019a; Gaiotto et al. 2020; Oe et al. 2020) and competition with native (Balzani et al. 2016) and other alien species (Balzani et al. 2020; Haubrock et al. 2020a). Moreover, it can be used to reveal the role of new alien prey in the diet of resident predators (Juarez-Sanchez et al. 2019; Stellati et al. 2019), compare trophic levels between introduced and native populations of invasive species (Balzani et al. 2021), as well as to disentangle trophic relationships among alien species in invaded communities (Haubrock et al. 2019a; Bissattini et al. 2021). Finally, SIA can be used to identify links between terrestrial and aquatic environments and depict changes in either one following alterations in the other (Gregs et al. 2014). However, the potential of SIA in this research field has not been fully explored yet (Bodey et al. 2011), and new applications have recently been suggested (McCue et al. 2020).

Predicting biotic interactions

Recently, SIA and associated mixing models have been proposed as a new and versatile approach in assessing potential risks arising from feeding pressure by invasive species, thus enabling to forecast the possible outcomes of the reintroduction of once native species (Haubrock et al. 2019b) and unravelling the role of species introductions on native species extinction (Haubrock et al. 2020b).

These seminal studies were carried out in an aquatic system, namely the model community of Lake Arreo, Northern Spain, which is currently dominated by alien species (Haubrock et al. 2018). In the first study (Haubrock et al. 2019b), the isotopic

niche of the European eel *Anguilla anguilla* from a German lake with a similar community composition (Dörner et al. 2009) was projected onto the isotopic community structure of Lake Arreo, where this fish species was once native. The aim was to assess the effectiveness of this predator as biocontrol agent for the aquatic alien species. To allow comparisons, data from both eel and the Arreo community were standardized using the baseline organism (primary producer, *Phragmites australis*) that occurs in both ecosystems. In the other study (Haubrock et al. 2020b), isotopic data from a vertebrate (the common tench *Tinca tinca*) and one invertebrate (a whirligig beetle *Gyrinus* sp.) species once native but now locally extinct, were extrapolated from suitable literature and projected in the community to model biological effects (predation, competition) that potentially lead to their demise.

As such, these studies determined a considerable biotic pressure, mostly driven by both predation from the occurring (introduced) top predator, the largemouth bass *Micropterus salmoides*, and competition with native and other introduced species. Furthermore, the potentially arising trophic web was conceptually depicted considering the potentially consumed prey of the reintroduced eel, and thus, its effect on the recipient community. These studies thereby highlighted the opportunity for a new research line that exploits the potential of isotopic data to assess specific impacts at local scales. For example, the analysis of isotopic niches and resource utilization can be used to predict interspecific interactions (i.e. either competition or predation) after the potential introduction of a global invader in other areas or locations.

Here, we propose the application of this approach as a tool to use within risk analysis frameworks, including horizon scanning and risk screening and further assessments, to prevent new invasions, and to optimize reintroduction as well as assisted migration efforts by assessing the probable trophic relationships arising. Therefore, we discuss the requirements, advantages, and assumptions of this application.

SIA impact assessment

Requirements

Trophic links between species are the result of specific local conditions, as for example the number of trophic levels and the biomass within each – and, thus, prey availability and competition – depend on the productivity of ecosystems (Leibold et al. 1997). Each community differs and is unique due to various factors such as species composition and abundance, behavioural differences and local adaptations, different energy pathways as well as connectance with the surrounding ecosystems, and ultimately abiotic variables (e.g. substrate, altitude, climate). Although consumers show a certain degree of behavioural and dietary plasticity (Lehmann et al. 2013; Svanbäck et al. 2015; Mavraki et al. 2020), it can be assumed that under similar abiotic conditions, communities with similar species would reflect similar trophic positions and structures (Haubrock et al. 2020b). Therefore, it is important to accurately choose

data from communities as similar as possible to the focal community (Haubrock et al. 2019b). Moreover, the standardization of isotopic data using local baselines (i.e. primary producers or, preferably, primary consumers) is needed to make data comparable (McMahon and McCarthy 2016). However, the two data sources should rely on the same energy pathway (i.e. terrestrial vs. aquatic, C3 plants vs. C4 plants), otherwise the result would lead to a meaningless confounding effect (Haubrock et al. 2020b). The goodness of the similarity can be checked by testing whether the projected data falls into the community total hull area (Layman et al. 2007) after being standardized (Haubrock et al. 2019b).

Beside spatial, also temporal differences in species diet and relative abundance (e.g. insects boosts) and consequently in community structure must be considered when choosing data. This refers to natural seasonal changes but also to the time since introduction for already established populations, as the diet of a species can change during its invasion process (Tillberg et al. 2007), depending on resource availability (Ruffino et al. 2011).

Finally, it is well known that the carbon isotopic signature is depleted by some compounds, mostly lipids (Post et al. 2007). A plethora of methods such as lipid chemical extraction have been used to deal with this bias (Arostegui et al. 2019). Therefore, isotopic data from samples treated in the same way are needed, whereas untreated and lipid-extracted samples should not be compared, because this could lead to misinterpretations due to the incorrect topology of the projected data in the isotopic space.

Advantages

There are three main advantages that this predictive method can offer. First, the impact of a potentially introduced alien species on the native community in terms of predation can be estimated using mixing models (Parnell et al. 2013). Knowing the species composition of the host community, mixing models will allow to estimate which taxa could be mostly preyed. If some of the mainly potentially preyed taxa are of conservation concern, this will result in a high potential impact. On the other hand, if sensitive taxa are not likely to be heavily preyed, this will reduce the risk associated with the potential introduction of a species.

Another important advantage is the estimation of feeding competition potentially occurring with other, already present, species. The overlapping resource use can be inferred by using models that investigate the proportion (Stasko et al. 2015) of potentially arising isotopic niche overlap (e.g. Bayesian or corrected standardized ellipse area or Kernel isotopic niche, Jackson et al. 2011; Eckrich et al. 2020). Isotopic niches are a multivariate (usually bidimensional) representation of the Hutchinson's n -dimensional ecological niche (Newsome et al. 2007). As discussed above, the niche defined by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ reflects the trophic niche, so the degree of trophic niche overlap provides an index of potential competition between species. When niches are overlapped to some degree, competition is likely to occur, particularly when trophic resources become limiting (Pianka 1981).

Finally, hurdles for the reintroduction of native species as well as assisted migration projects can be identified and addressed a priori given the composition of the community where the reintroduction is planned (Haubrock et al. 2020b), informing the choice of most suitable sites where these actions will be most likely to succeed, minimizing the management costs and maximizing the success probability.

Assumptions

The most important assumption this approach relies on is the niche conservatism of the focal species. The trophic niche of a species in different ecosystems can vary (especially for generalist species) depending e.g. on the availability of different resources, community composition and habitat type (Balzani et al. 2021; Haubrock et al. 2021a,b) and ultimately on climate change (Bestion et al. 2019). Moreover, invasive species are known for their plasticity (Courant et al. 2017; Loureiro et al. 2019; Rolla et al. 2020), thus limiting the reliability of predictive modelling. Despite this, consistent patterns in feeding preferences of introduced populations have been well documented in some invasive species (Tillberg et al. 2007; Wilder et al. 2011). To address this issue, we suggest the use of data from other invasive populations, when available, as these can provide more reliable predictions (Barbet-Massin et al. 2018). However, these assumptions are the same as for other existing tools used in the prevention of potentially invasive species. Indeed, both predictive models and risk assessment protocols use information (e.g. behavioural or biological traits, impacts) on a species from its native or introduced ranges and project this information to predict potential impacts and geographic spread that could arise (Bacher et al. 2018; Roy et al. 2019; Liu et al. 2020).

Second, species should be at equilibrium in their new range and maintain their ecological niche (Gallien et al. 2012; Hattab et al. 2017). Moreover, the output is highly sensitive to uncertainties, errors, and deficient data (Katsanevakis and Moustakas 2018). Even the suggested species distribution model implementation using eDNA similarly presents some limits and potential biases (Muha et al. 2017). Alternative approaches have been proposed, such as comparative functional responses (Dick et al. 2017a,b), that showed predictive power across multiple study systems comprising different taxonomic groups and geographic regions (Cuthbert et al. 2019). Further, this approach allows the rapid assessment of ecological impacts, while incorporating context-dependencies such as warming (Haubrock et al. 2020c) and can be combined with field abundances and reproductive traits to scale-up and predict population-level impacts (Dick et al. 2017a; Dickey et al. 2020). However, the general applicability of this method to measure the impacts of a species remains debated (Dick et al. 2017c; Vonesh et al. 2017a, b). Nevertheless, these tools can provide good predictions, especially when data are derived from other invasive populations (e.g. Barbet-Massin et al. 2018).

True limitations are linked to stable isotope data availability, however with the increase in SIA studies, the available data are rapidly increasing, offering new opportunities. Pauli et al. (2015, 2017) have called for a global stable isotope database, which

would prove very useful in this context, together with open access publications and data repositories. If data are available, further information can be considered to refine the predictions. For instance, stable isotope data of a potential prey species could be partitioned according to size classes to improve the resolution of applied mixing models, and predators' diet, gape size or habitat use could be used as priors in Bayesian mixing models. Such a repository for isotopic data (IsoBank) has recently been launched (<https://isobank.tacc.utexas.edu/>), making feasible all the possibilities above discussed.

Application and potential outlook

With all the discussed potential insights provided by SIA-based risk assessments to improve management programmes, this approach potentially presents a unique way to inform practitioners in the fields of biological invasions and conservation biology to better inform stakeholders and governmental institutions. In practical terms, SIA-based risk assessments could be integrated in already existing tools such as EICAT and/or SEICAT as well as AS-ISK (Hawkins et al. 2015; Copp et al. 2016; Bacher et al. 2018), which have been widely adopted (also in combination, see Haubrock et al. 2021c), and new *ad hoc* tools can also be developed.

Other future developments could derive from this conceptually simple framework. For example, the availability of present and past environmental data, as well as future predictions (under climate change scenarios), integrated with SIA on museum samples will allow to include a temporal view on this approach, considerably improving its accuracy.

One interesting avenue that will surely show its potential in the invasion ecology field is the compound-specific stable isotope analysis (CS-SIA) of amino acids. In the context of our theoretic framework, this promising recent methodology will undoubtedly help in solving the issue of data standardisation and availability. This technique allows a more precise estimation of a consumer's trophic position based solely on the consumer's amino acid isotopic ratios (Chikaraishi et al. 2009). This releases the isotopic data from the need to be referenced by a correct baseline to be useful for projections. Indeed, the baseline presents potentially large spatial and temporal variations that are reflected in primary producers and, consequently, in upper trophic levels along the food web (Ishikawa 2018). CS-SIA makes the isotopic data from different populations directly comparable and increases the usable datasets (i.e. including those without baseline data available). Another advantage of CS-SIA is that different tissues do not present different isotopic signatures (e.g. Chérel et al. 2019), leading to an "absolute" isotopic signature of the animal. This also favours the usability and comparability of data from different tissues, without the need of utilising the same tissue. Further, CS-SIA on museum specimens can be used to reconstruct past food webs, helping in management and restoration efforts (Blanke et al. 2018). Although this technique is still costly, the decreasing costs of eDNA analysis suggest similar price reductions for the application of CS-SIA in the near future.

Conclusions

Projecting stable isotope data onto the isotopic space of the focal community has the potential to predict impacts accompanying a newly introduced species as well as the success of species reintroduction and assisted migration. Despite some required assumptions, the approach can have high utility from a scientific as well as management perspective by identifying trophic biological impacts of a wide range of taxonomic groups and habitats. Such results can thus be used to inform risk-based management programmes and make an important contribution to impact assessments, allowing a better prioritisation. Finally, optimising the chances of success of reintroduction as well as assisted migration efforts, will turn in a considerably better resource utilization.

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