Using stable isotope analysis to answer fundamental questions in invasion ecology: Progress and prospects

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Abstract

1. What makes some species successful invaders while others fail, and why some invaders have major impacts in invaded ecosystems are pivotal questions that are attracting major research effort. The increasing availability of high resolution, georeferenced stable isotope landscapes ('isoscapes'), coupled with the commercialization of stable isotope-enriched tracer molecules and the development of new analytical approaches, is facilitating novel applications of stable isotope techniques in ecology. We can now address ecological questions that were previously intractable.

2. We review and discuss how stable isotope analysis (SIA) can complement fundamental research themes in the study of biological invasions, especially in answering questions relating to the physiological and ecological mechanisms underlying invasion processes and invader impacts.

3. SIA was first used for simply describing the diet of invaders but, more recently, SIA-informed metrics of population and community trophic structure have been advanced. These approaches now permit the comparison of diets across space and time and provide quantitative tools to compare food webs across different stages of invasion.

4. SIA has also been pivotal in quantifying competition for resources between native and non-native species (e.g. competition for food, water, or nutrient use). Specific questions related to modes of dispersal (e.g. origin and distance/direction travelled) and mechanisms of establishment can also be addressed using SIA in diverse taxa.

5. An overarching goal is to highlight examples of recent studies that have used SIA in key areas of invasion ecology and use these to synthesize testable predictions where SIA could be applied to future studies. We conclude by highlighting several paths forward and describing how unresolved challenges in quantifying the rates, impacts, and mechanisms underlying invasions could potentially benefit from the use of SIA.

1 | INTRODUCTION

1.1 | Biological invasions

The phenomenon of biological invasion involves the transport of organisms through human activity to areas outside their current native range (as defined by adaptation, natural dispersal mechanisms and biogeographical barriers) and their performance in the novel range, including their ability to survive, establish, reproduce, spread, proliferate and interact with resident biota (Hui & Richardson, 2017).

Invasions of plant and animal species are taking place at unprecedented rates in every type of ecosystem, with no apparent saturation in the number of species being introduced (Roques, 2010; Roques et al., 2016; Seebens et al., 2017; Westphal, Browne, MacKinnon, & Noble, 2007). Substantial progress has been made in elucidating many facets of invasion ecology (Hui & Richardson, 2017; Richardson, 2011). Despite this, the rapid changes in community structure and ecosystem function that often follow an invasion are highly variable, context-dependent and are, in most cases, poorly understood (Bellard, Cassey, & Blackburn, 2016; Jeschke et al., 2014; Kenis et al., 2009; Kumschick et al., 2015; Parker et al., 1999; Strayer, Eviner, Jeschke, & Pace, 2006). Huge challenges remain with respect to understanding the fundamental mechanisms by which invasions occur and characterizing the specific ecological impacts invaders have on ecosystems.

The burgeoning literature on invasion ecology has generated many 'invasion frameworks' that classify and categorize the key mechanisms and processes that mediate invasions (e.g. Jeschke & Heger, 2018). Biological invasions are usually not single discrete events, but rather involve a progression of sequential events. At each stage of an invasion, introduced populations must overcome a series of geographic, physiological and ecological barriers (Allendorf & Lundquist, 2003; Blackburn et al., 2011; Richardson, Allsopp, D'Antonio, Milton, & Rejmanek, 2000; Simberloff & Von Holle, 1999). The effectiveness of these barriers may be significantly reduced if (a) a species is pre-adapted or otherwise well suited to climatic and edaphoclimatic conditions in the novel range (Curnutt, 2000); (b) a species experiences advantages stemming from enemy release (Keane & Crawley, 2002; Maron & Vila, 2001) or co-introduction of beneficial partners (Le Roux, Hui, Keet, & Ellis, 2017); or (3) human-induced changes facilitate invasion (Hufbauer et al., 2012). Regardless of the precise mechanisms, it is increasingly evident that understanding these complex processes requires researchers to employ a wide range of approaches (Hui & Richardson, 2017; Vas et al., 2017).

1.2 | Stable isotope analysis

Stable isotope analysis (SIA) provides a powerful tool to explore many of the mechanisms implicated in invasion dynamics, and for testing many hypotheses and theories in invasion ecology. Stable isotopes are not radioactive and naturally occur in every environment and organism. The isotopic signature of a sample refers to the proportion of different atoms of the same element that have different atomic masses found in tissue or a substance. These signatures can be influenced by photosynthetic pathway, diet composition, water sources and various environmental conditions. Stable isotopes common to all organisms [carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), sulfur ($^{34}S/^{32}S$), hydrogen ($^{2}H/^{1}H$), and oxygen ($^{18}O/^{16}O$)] can therefore be used to measure dispersal patterns and pathways of invasion, quantify resource investment into growth and reproduction and characterize the effects of invasions throughout food webs.

Stable isotope analysis has become an increasingly popular tool among ecologists, and isotopic ecology has become a productive research field in its own right (Hobson & Wassenaar, 1999; Martinez del Rio, Wolf, Carleton, & Gannes, 2009). Variation in naturally occurring stable isotopes (Box 1) can be used to study food web dynamics in diverse ecosystems and has long been appreciated in general ecology (Gannes, O'Brien, & Martinez del Rio, 1997; Martinez del Rio et al., 2009). Although several studies have employed SIA to investigate biological invasions (reviewed in Bodey, Bearhop, & McDonald, 2011), its use remains sporadic (but see Kamenova et al., 2017). The increasing availability of georeferenced, high-resolution stable isotope landscapes ('isoscapes'; sensu Bowen, Liu, Vander Zanden, Zhao, & Takahashi, 2014; Cheesman & Cernusak, 2016; West, Bowen, Dawson, & Tu, 2010; West, Sobek, & Ehleringer, 2008) [e.g. groundwater (West, February, & Bowen, 2014); marine (Magozzi, Yool, Vander Zanden, Wunder, & Trueman, 2017); and precipitation (Terzer, Wassenaar, Araguas-Arags, & Aggarwal, 2013)] and the commercialization of stable isotope-enriched organic 'tracer' molecules (e.g. monosaccharides, amino acids, fatty acids) for artificial enrichment studies (e.g. Cambridge Isotope Laboratories, ISOTEC-Sigma Aldrich) provide new applications for SIA.

It is currently possible to artificially enrich thousands of different molecules with stable isotopes (McCue & Welch, 2016) which, when purified, can be used as tracer molecules to isotopically enrich plants and animals to track the flow of specific resources or propagules through ecosystems. The past two decades have seen the cost of commonly used tracers decrease dramatically; highly enriched ^{13}C-glucose, for example, is less than $100 per gram (Hood-Nowotny & Knols, 2007). Over the same time, the development of laser-based isotope analyzers allows users to make measurements in near-real time with higher throughput and lower costs (McCue & Welch, 2016; Voigt, 2009; Welch, Perronet, Voigt, Hatch, & McCue, 2016). The direct integration of SIA with chromatography systems and other molecular separation techniques now enables researchers to conduct compound-specific SIA (quantification of stable isotope

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BOX 1 Fractionation

Fractionation is the result of physicochemical forces that cause differential abundances of heavy and light isotopes throughout the environment (i.e. isoscape) and within the organism which allows ecologists to make predictions about where an animal has been, or what it is eating. Some common variations in isotope signatures are:

- Naturally occurring differences in H and O isotopic signatures in the environment are primarily the result of equilibrium fractionation (e.g. phase changes of water) (Fry, 2006; IAEA, 2000; Werner et al., 2012). H signatures might also present information about trophic status within a given food chain (Vander Zanden, Soto, Bowen, & Hobson, 2016).
- Plants exploiting C_3 and C_4 photosynthetic pathways exhibit kinetic fractionation (e.g. during biochemical reactions) and differentially fractionate against CO_2 molecules with different isotopic composition (e.g. $^{13}CO_2$ and $^{12}CO_2$) (O'Leary, 1988; O'Leary, Madhavan, & Paneth, 1992; Whelan, Sackett, & Benedict, 1973). In short, C_3 plants discriminate more against $^{13}CO_2$ and thus contain measurably lower levels of ^{13}C in their tissues.
- Marine-derived carbon is isotopically variable (Farquhar, Ehleringer, & Hubick, 1989), but tends to contain ^{13}C levels that are higher than terrestrial-derived carbon (Chisholm, Nelson, & Schwarcz, 1982; Inger & Bearhop, 2008; Quillfeldt, Bugoni, McGill, Masello, & Furness, 2008; Rubenstein & Hobson, 2004; Schimmelmann, 2011).
- Nitrogen accounts for approximately 6% of the mass of all proteins. The most commonly studied fractionation pattern is trophic enrichment, where the proteins in heterotrophs become more enriched than the protein they consume in their diets due to preferential retention of the heavy isotopes during tissue renewal (Caut, Angulo, & Courchamp, 2009; Hobson, Schell, Renouf, & Noseworthy, 1996; Kelly, 2000; Post, 2002).
- ^{15}N levels in marine ecosystems also tend to be higher than IN terrestrial (Coplen et al., 2002; Evans Ogden, Hobson, & Lank, 2004; Grey, Waldron, & Hutchinson, 2004; Nardoto et al., 2006).
- Nitrogen-fixing plants, mostly legumes, typically have lower levels of ^{15}N since the enzyme responsible for biological N-fixation by rhizobia, nitrogenase, preferentially incorporates the lighter isotope of atmospheric N_2 gas (Unkovich, 2013). Invasive legumes including *Acacia* spp. may have ^{15}N levels in leaf tissues that are higher than native species (Rascher, Hellmann, Maguas, & Werner, 2012).

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distributions among individual amino acids or fatty acids in a tissue sample) (e.g. Chamberlain, Bull, Black, Ineson, & Evershed, 2004; Chikaraishi, Naraoka, & Poulson, 2004; Cifuentes & Salata, 2001; McCarthy, Benner, Lee, & Fogel, 2007; McClelland & Montoya, 2002).

To our knowledge, no studies have documented reduced fitness or deleterious long-term effects of stable isotope tracers in free-living organisms (unlike radioactive isotopes e.g. Braden, Lembcke, & Caspary, 2007). The analytical methods for measuring and reporting stable isotope values are well established but are beyond the scope of this review; readers interested in learning such fundamentals can find several excellent reviews on the topic (Coplen et al., 2002; Farquhar et al., 1989; Gannes, Martinez del Rio, & Koch, 1998; Hayes, 2001; McCue, 2011; McKechnie, 2004; O'Brien, 2015; Peterson & Fry, 1987; Thompson, Bury, Hobson, Wassenaar, & Shannon, 2005).

This paper summarizes some of the most elegant and informative uses of SIA in field and laboratory studies and describes new applications for SIA to answer fundamental questions in invasion science with focus on examples of how such approaches could elucidate the physiological and ecological mechanisms underlying invasions and invader impacts. We also highlight how researchers can use differences in the natural abundances of stable isotopes as well as purified tracer molecules to address key questions in invasion ecology.

2 | DISPERSAL

2.1 | Natural abundance approaches

Dispersal is a critical aspect of invasions both for overcoming barriers to becoming established in new environments and for determining the subsequent geographical spread of an invasive species once it has become established (Trakhtenbrot, Nathan, Perry, & Richardson, 2005). Stable isotopes (particularly ^2H and ^{18}O) have been extensively used to trace origins and migration patterns of individuals across large spatial scales (Graves, Romanek, & Rodriguez-Navarro, 2002; Heinrich & Collins, 2016; Hobson, 1999; Inger & Bearhop, 2008; Rubenstein & Hobson, 2004). Natural differences in isotopic abundance result from different assimilation rates which generate slight geographical variations in isotopic signature. These variations can then be used to trace migration or dispersal patterns. The approach relies on known and predictable variations in the isoscape or an isotope boundary (Hood-Nowotny & Knols, 2007). For example, researchers recently found that the ^2H in the bodies of invasive Japanese beetles were closely correlated with ^2H in local precipitation across the USA and that their isotopic signatures changed predictably when exposed to simulated geographic changes in their water supply (Hungate et al., 2016). Others have used similar approaches to track discrete waves of invasions of Asian longhorned beetles

(Heinrich & Collins, 2016). These studies demonstrate the potential for tracking the timing of populations arriving at new locations and monitoring the efficacy of dispersal control and management measures in near-real time.

Geographic variation in isotopes may elucidate invader dispersal over very long distances across variable isoscapes (such as human-mediated dispersal events that lead to introduction), but naturally occurring variation may be insufficient to unravel shorter distance dispersal events. Fortunately, high-resolution isoscape maps are becoming more widely available and, as more types of isotopes are surveyed (e.g. Phillips, 2012; Phillips & Gregg, 2003; West et al., 2014), the potential for addressing dispersal-related questions at smaller scales is increasing because a greater number of axes can be used to distinguish locations.

A key advantage of SIA in dispersal studies of animals is that it can be performed in a single capture event. In short, there is no need to catch, mark, release, and recapture specimens in the environment to estimate dispersal. This is crucial, because such experimental methods are often impractical or illegal for invasive species in their invaded range. In some cases, museum specimens may also be utilized if the preservation process does not introduce significant analytical bias. In fact, numerous studies have conducted SIA on tissues from museum/stored collections (Doucett, Giberson, & Power, 1999; Maguire & Grey, 2006; Murphy, Bowman, & Gagan, 2007; Schmidt, Olden, Solomon, & Vander Zanden, 2007). For many taxa this is a key advantage, because it can allow easy access to a large number of specimens collected over long periods and from many localities (e.g. Heinrich & Collins, 2016; Hungate et al., 2016; Tillberg, Holoway, LeBrun, & Suarez, 2007).

The dispersal of many invasive animals may be difficult to study both in their native and invaded range due to their remote locations or cryptic behaviours. Conventional techniques [e.g. mark-recapture, telemetry, occurrence patterns, genetic studies (Ranius, 2006)] are time consuming and costly methods of measuring the dispersal patterns of invasive species compared to SIA (Bodey et al., 2011). Moreover, in cases where ethical considerations prevent collection or euthanizing large numbers of animals, small subsamples of tissues can be used for SIA. Common examples include feathers in birds (Pekarsky et al., 2015; Prochazka, Wilgenburg, Neto, Yosef, & Hobson, 2013; Rubenstein & Hobson, 2004), fur or whiskers in large carnivores (Mutirwara, Radloff, & Codron, 2017; Voigt et al., 2014; Yeakel et al., 2009), or baleen of whales (Aguilar, Gimenez, Gomez-Campos, Cardona, & Borrell, 2014; Schell, Saupe, & Haubenstock, 1989). As discussed below, SIA can even be used to track dispersal patterns of plant seeds.

2.2 | Artificial enrichment approaches

Another area where SIA can be employed to tackle dispersal-related questions in invasion ecology is through the use of *artificial enrichment* – a method that is perhaps especially well-suited to answer questions surrounding 'fine-scale' (e.g. <1 km) dispersal of both plants and animals. Sessile, seed-dispersed plants represent a particularly challenging situation for estimating landscape-scale

dispersal. To what extent do dispersal patterns differ between native and invasive species? Indirect approaches like genetic parentage or gene flow estimates are often used as surrogates to infer dispersal (Ouborg, Piquot, & van Groenendael, 1999). However, these are not only expensive, but also only provide crude dispersal estimates, since rare long-distance dispersal events often go undetected (but see e.g. Schmidt, Filipović, Hoffmann, & Rašić 2018).

Artificial enrichment involves integrating into the diet, or externally applying, isotope-enriched compounds with an isotopic signature that is different from the natural environment. This method has proven to be an efficient tool for tracking the dispersal of the invasive Amur honeysuckle shrub using topical (foliar) applications of ^{15}N-enriched urea (CH_4N_2O) to the maternal plant (Castellano & Gorchov, 2013). The authors assessed three concentrations of application across five time points (every three weeks) and then collected seeds and split these into those that were measured for ^{15}N and those allowed to germinate and grow under various conditions. Remarkably, even a single foliar application of ^{15}N was sufficient to effectively isotopically label both the seeds and the tissues of subsequent seedlings of this invasive shrub.

Other researchers have added ^{15}N-labelled ammonia (NH_4) to freshwater ponds and rivers inhabited by stonefly and mayfly larvae. The larvae consumed the ^{15}N-enriched detritus, resulting in adult flies that were isotopically distinct from natural populations but otherwise identical (Figure 1f). Traps placed around the ponds then allowed researchers to document the timing, distance, and direction of dispersal (Hershey & Pastor, 1993; MacNeale, Peckarsky, & Likens, 2004, 2005). It has even been proposed that sangivorous insect vectors (e.g. mosquitos, tsetse flies, *etc*.) can be captured and fed isotopically enriched blood meals before being released to track dispersal, habitat range, *etc*. (Hood-Nowotny & Knols, 2007). We know of no invasion studies that have employed this method in the field, most probably due to legal constraints when releasing the species in its invaded range.

Artificial enrichment can also be used to identify long-distance dispersal within the invaded range. Long-distance dispersal (e.g. >1 km) is a key process underlying some biological invasions, enabling rapid dispersal, fast population growth, and sampling of suitable habitat across the new range (Higgins & Richardson, 1999). Identifying areas that are most likely to receive long distance-dispersed propagules is crucial for effective management (Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009). A ^{15}N-enrichment approach used to track long-distance seed dispersal of native populations of the European holly and hawthorn tree elegantly illustrates the context (habitat) dependency of dispersal events for these two species and showed the need to consider habitat heterogeneity to manage ecological connectivity of landscapes (Carlo, Garcia, Martinez, Gleditsch, & Morales, 2013).

3 | DIET AND NICHE SPACE

Following introduction, the establishment and spread of a non-native species depends on it being able to extract sufficient nutrients
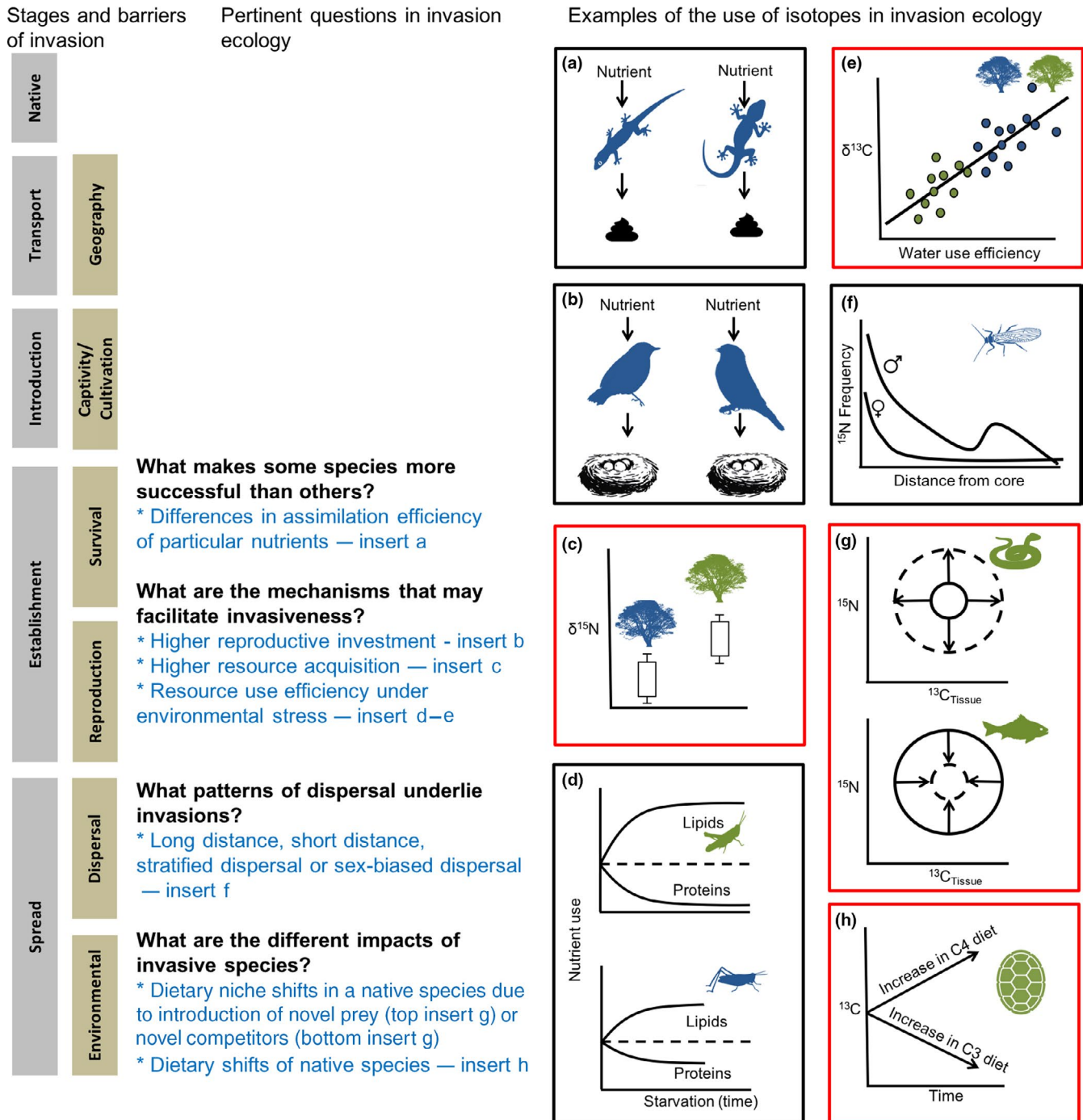
Stages and barriers of invasion	Pertinent questions in invasion ecology	Examples of the use of isotopes in invasion ecology

Stages and barriers of invasion:
- Native
- Transport — Geography
- Introduction — Captivity/Cultivation
- Establishment — Survival / Reproduction
- Spread — Dispersal / Environmental

Pertinent questions in invasion ecology:

What makes some species more successful than others?
* Differences in assimilation efficiency of particular nutrients — insert a

What are the mechanisms that may facilitate invasiveness?
* Higher reproductive investment - insert b
* Higher resource acquisition — insert c
* Resource use efficiency under environmental stress — insert d–e

What patterns of dispersal underlie invasions?
* Long distance, short distance, stratified dispersal or sex-biased dispersal — insert f

What are the different impacts of invasive species?
* Dietary niche shifts in a native species due to introduction of novel prey (top insert g) or novel competitors (bottom insert g)
* Dietary shifts of native species — insert h

FIGURE 1 Main research questions pertaining to how introduced species progress along the introduction-naturalization-invasion continuum. The role that stable isotope analyses may play in answering these questions are depicted as hypothetical examples. Note that most taxon comparisons are between native (green) and invasive alien (blue) taxa (e.g. inserts c–e) but that most approaches can also be applied between different invasive alien taxa (e.g. insert a–b) to assess differential invasiveness, impacts, etc. Examples of mechanisms that utilize natural isotopes are shown in red boxes and those making use of artificially enriched isotopes in black boxes

from the environment to support its continual mass and energy demands associated with growth, survival, and reproduction. Understanding invader diets helps in identifying specific physiological traits that contribute to (or limit) invasion success. Such insights are needed to inform predictions about the impacts of invaders on native communities, and to identify potential management options.

The ^{13}C, ^{15}N, and ^{34}S in animal tissues reflect dietary resources – essentially 'you are what you eat' (sensu DeNiro & Epstein, 1976). SIA is, therefore, an ideal tool for characterizing dietary history. It has the added advantage that it provides longer-term estimates than acute behavioural observations or stomach content analyses, which only give 'snapshots' in time.

3.1 | Dietary flexibility

To what extent are invasive species capable of tolerating changes in their diet? SIA has been used to show that invasive ants vary their diet across seasons, by rapidly exploiting periodic pulses in floral nectar availability (Mothapo & Wossler, 2017). Another study found that introduced populations of the invasive carnivorous Argentine ant initially occupied a similar trophic level to native Argentinian populations (Tillberg et al., 2007). However, once established, the invasive ants shifted to a lower trophic position as they consumed a greater proportion of plant-based resources (e.g. nectar and honeydew) following the drastic reductions in native Californian ant populations in the face of their invasion. Similar trophic flexibility was found in invasive red swamp crayfishes, where ^{13}C signatures revealed that they maintained a competitive advantage over native species during food shortages by increasing consumption of allochthonous riparian vegetation (Grey & Jackson, 2012), and in invasive rats on Surprise Island in New Caledonia, that consumed seabird chicks when available, but switched to sea turtle hatchlings when seabirds were not present (Caut, Angulo, & Courchamp, 2008). Similar evidence from studies in aquatic environments indicates that invasive species often have a flexible and generalist diet (e.g. Garton, Payne, & Montoya, 2011; Jackson, Wasserman, et al., 2017; Zhang et al., 2010). Further isotope studies on invasive species across a variety of habitat types, and comparative studies between invasive and native congeners, are needed to determine the universality of such dietary flexibility and responses to resource availability among invasive species. SIA is particularly well-suited to detect subtle differences in resource use patterns, particularly in marine habitats where it is difficult to directly observe animals. For instance, SIA has been used to identify previously unknown feeding ecotypes within populations of amphipods (Nyssen, Brey, Dauby, & Graeve, 2005), delphinids (Kiszka, Oremus, Richard, Poole, & Ridoux, 2010), and penguins (Cherel & Hobson, 2007). Such characteristics could even be altered at different stages of biological invasion (see below).

3.2 | Trophic interactions between invaders and natives

In the last decade, ecologists have developed numerous stable isotope-derived metrics to quantify population and community trophic ecology. For instance, the metrics 'Total Area' (Layman, Arrington, Montana, & Post, 2007) and 'Standard Ellipse Area' (Jackson, Inger, Parnell, & Bearhop, 2011) can be used to quantify the spread of individuals in isotopic space as a measure of niche width (Figure 1g). Several studies have used these metrics in invasion ecology. For instance, researchers showed that invasive crayfish have a wider niche width than their native counterparts (Olsson, Stenroth, Nystrom, & Graneli, 2009). Another study reported changes in niche overlap between invasive and native fish (Hill, Jones, Hill, & Weyl, 2015). Isotopic niche space can also be detected through shifts in centroid location, or a change in variance (Bearhop, Adams, Waldron, Fuller, &

Macleod, 2004; Bond, Jardine, & Hobson, 2016; Guisan, Petitpierre, Broennimann, Daehler, & Kuaffer, 2014; Hammerschlag-Peyer, Yeager, Araujo, & Layman, 2011; Turner, Collyer, & Krabbenhoft, 2010).

Estimates of isotopic niche width across an invader's range, and at different stages of invasion, can even be used to predict invader impacts (Comte, Cucherousset, & Olden, 2017), and to inform decisions about appropriate control or eradication plans. For example, lake productivity and size were shown to alter the trophic position and isotopic niche width of invasive red swamp crayfish (Jackson, Evangelista, et al., 2017). Studies of stable isotope niche space also show that invasions can have cascading effects, altering the niche width of other invaders or native species. For instance, eight years of isotope data during the establishment of invasive carp revealed that invasion by this fish caused a reduction in the dietary niche of a previously established invasive crayfish (Jackson et al., 2012).

3.3 | Large-scale food web effects

Biological invasions inevitably cause shifts in food web structure since they automatically add a new 'node' (i.e. the invasive species) and thus new 'links' [i.e. their feeding interactions (Jackson, Wasserman, et al., 2017)]. These changes can alter ecosystems in several ways and across multiple levels of organization (from individuals to ecosystems), and multiple trophic levels (Cucherousset & Villeger, 2015; Hette-Tronquart, 2019). For instance, invasive predators can have conspicuous direct effects on their prey, with cascading consequences for lower trophic levels. Invaders may also have 'bottom-up effects' on the food web (i.e. acting as a novel food source) or they may compete with native species for resources (Jackson, Wasserman, et al., 2017). Researchers gathered 4,030 isotopic values for fish from 496 communities to assess invasive fish impacts and found that the presence of invasive species invariably alters isotopic community structure, but that the effects differed across ecosystem type (Sagouis, Cucherousset, Villeger, Santoul, & Boulentreau, 2015). For example, in running waters, the non-natives (primarily predators) increased the total community isotopic niche without altering the niche breadths of native fish species. In still waters, non-natives modified basal resource consumption and reduced the isotopic niche breadths of natives through competition.

In one of the first applications of SIA in invasion ecology, researchers showed that invasive smallmouth bass and rock bass caused a shift in trophic position and dietary habitat use of native lake trout (Vander Zanden, Casselman, & Rasmussen, 1999). Another study indicated that zooplankton gradually became more reliant upon terrestrial detritus when filter feeding zebra mussels invaded a lake in Ireland where they competed for algal resources (Maguire & Grey, 2006). SIA has since been used to demonstrate that the ecological effects of invasions can cascade across ecosystem boundaries. For instance, a study of ^{13}C and ^{15}N revealed the far-reaching effects of invasive fish on the diets of terrestrial

spiders (Jackson, Woodford, et al., 2016). Another study used measures of ^{15}N to show that seabirds enhance coral reef productivity in the absence of invasive rats on islands (Tabak et al., 2016). Soils and coastal shrubs on rat-free islands were highly enriched in ^{15}N compared to rat-infested islands, reflecting pelagic nutrients transferred by seabirds. This higher δ^{15}N was also found in microalgae, sponges, and herbivorous damselfish on adjacent coral reefs. Researchers recently demonstrated that co-invasion of a bivalve with invasive corals does not involve nutritional links, but rather that the invasive coral creates habitat that facilitates co-invasion of the mussel (Vinagre et al., 2018). Additional examples of this phenomenon known as 'invasional meltdown' are discussed in Section 5.

3.4 | Considerations for diet analyses

The pressures that drive changes in niche space can differ with ontogeny and may occur at different times within the lifetime of long-lived species (Cherel, Fontaine, Jackson, Jackson, & Richard, 2009; Hammerschlag-Peyer et al., 2011). It is therefore important to measure tissues whose elemental turnover rate reflects the period of interest (e.g. Ayliffe et al., 2004; Bauchinger & McWilliams, 2009; Church et al., 2009; Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015). For example, blood plasma or liver tissues tend to reflect recently consumed foods whereas muscle or connective tissues tend to integrate dietary history over longer periods (Schell et al., 1989; Tieszen, Boutton, Tesdahl, & Slade, 1983). Researchers showed that after a diet shift the δ^{13}C of metabolically active tissues (e.g. body fat or reproductive organs) changed faster than more metabolically inert tissues, and that the speed of change can differ between sexes (Gratton & Forbes, 2006). In the Japanese beetle study described above, researchers noted that although the isotope signatures of their whole bodies changed those of the wing and elytra tissues remained constant (Hungate et al., 2016). Such tissue-level differences are fortuitous because they reflect the isotope signatures of both the larval conditions and that of the new habitat.

Besides depicting the diet and niche space of invasive species, SIA can also be used to detect whether native species use invasive species as food resources in different regions, populations, and across time. Some animals such as tortoises are unique in that they 'record and carry' decades of isotopic data in their scutes (Figure 1h). By measuring ^{13}C and ^{15}N in keratinized growth rings of tortoise shells researchers showed that individuals used plant resources very differently across years (Murray & Wolf, 2013). For example, some individuals in drier areas showed episodic shifts between diets that incorporated plants with C_3 or C_4/CAM photosynthetic pathways while other individuals in wetter areas had a more constant diet with higher reliance on C_3 plants across their lifetime. It is thus possible to detect dietary shifts and to reconstruct diet history or seasonality of tortoises inhabiting areas with invasive plants or along a plant invasion gradient. Despite

the potential of this approach, the isotopic values of growth rings are not purely discrete and carbon from a new diet can be incorporated into older rings ('carbon creep') – especially those adjacent to the new rings formed after the diet switch (Murray & Wolf, 2012). Therefore, this methodology requires calibration and cautious interpretation of isotope chronologies in addition to species-specific parameter estimates given the variation in different tissues' turnover rates and discrimination values among reptiles (Reich, Bjorndal, & Martinez Del Rio, 2008; Rosenblatt & Heithaus, 2013). Overall, the use of SIA to monitor dietary changes over long time spans should be further explored to quantify how invasion-induced niche shifts are correlated with other variables such as the warming climate and ongoing habitat loss thereby providing insight into how these multiple stressors interact.

4 | PHYSIOLOGICAL DIFFERENCES BETWEEN INVADERS AND NATIVE ANIMALS

4.1 | Assimilation efficiency

Animals are unable to absorb all the nutrients they ingest. Invasive species that can maximize nutrient uptake may have an advantage over others, possibly increasing their potential success. Overall, differences in dietary nutrient assimilation could have profound effects on the survival and persistence of an invader and it is possible to compare assimilation efficiencies between native and invasive animals. We discuss water uptake and nutrient assimilation of plants below, but the following questions generally apply to both groups. Do successful invaders have higher dietary assimilation efficiencies? If so, does this pattern apply to all classes of macronutrients equally? SIA offers an opportunity to answer these physiological questions.

Traditionally, dietary assimilation efficiency of animals has been studied by calculating differences between gross energy intake and the energetic content of excreta (e.g. faeces and urates). SIA can expand existing approaches by further allowing researchers to quantify digestive assimilation efficiency of different diets and even different nutrients. In practice this is done by feeding animals meals (supplemented with specific ^{13}C- or ^{15}N-labeled molecules) and then measuring the amount of the tracer recovered in the animals' wastes (e.g. breath, feces, urates, etc.; Figure 1a). For instance, sphinx moths (Levin, McCue, & Davidowitz, 2017) and house sparrows (McCue et al., 2011) had far higher assimilation efficiencies of dietary amino acids than fatty acids (Levin et al., 2017). Similarly, a study with humans used this approach to show that cooked egg proteins had much higher assimilation efficiencies than raw egg proteins (Evenepoel et al., 1999).

The specific type of tracer molecules used can vary depending on the type of macromolecules (e.g. carbohydrates, lipids, or proteins) thought to be limiting in the diet. The choice of isotope tracer (e.g. ^{13}C or ^{15}N) used in feeding studies can also provide unique

perspectives into nutrient dynamics. ^{13}C-labelled dietary tracers provide a good proxy of bulk energy assimilation for a given class of macronutrients. They also have the advantage of providing simultaneous information about the rates of oxidation for dietary nutrients if combined with ^{13}C-breath testing (see below). For example studies of reptiles showed that postprandial lizards (Plasman, McCue, Reynoso, Terblanche, & Clusella-Trullas, 2019) and pythons (McCue, Passement, & Guzman, 2015) oxidized a much greater proportion of dietary proteins than lipids.

^{15}N-labeled tracer molecules (e.g. amino acids) provide an excellent proxy of protein assimilation because nitrogen is generally absent from lipids and carbohydrates. Although the ^{15}N tracer cannot be detected in the exhaled breath, it can be readily measured in the faeces and urates (e.g. Balter, Simon, Fouillet, & Lecuyer, 2006; Carter et al., 1994; Hawkins, 1985; Sponheimer et al., 2003). Moreover, because nitrogen is far less abundant in the diet than carbon, a given dose of ^{15}N-labelled amino acid will give a stronger isotopic 'signal' than an equivalent, singly-^{13}C-labelled amino acid (Durso & French, 2017; Gaudichon et al., 1999).

4.2 | Energy use during resource limitation

Invasive species establishing new populations may experience forms of food or water stresses that may differ from what they have faced in their historical evolutionary contexts. In new habitats, these stressors could also occur at different frequencies or have different durations compared to their native range. One of the most commonly documented organismal responses to food or water stress is to behaviourally reduce activity and physiological functionality to minimize metabolic rates as occurs during hibernation, estivation, dormancy, diapause or starvation-induced hypometabolism (Geiser, 2004; Hohtola, 2012; McAllen & Geiser, 2014; McCue, 2010; McKechnie & Mzilikazi, 2011; Ruf & Geiser, 2014; Storey & Storey, 1990); but no animals can completely eliminate these costs.

Researchers can isotopically label discrete carbon pools in the body of animals (e.g. by repeatedly feeding them with meals artificially enriched with ^{13}C-labelled lipids or proteins) and conducting ^{13}C-breath testing (i.e. measurements of $^{13}CO_2$ release in the exhaled breath) to explore how they alter their reliance on their different types of metabolic fuels (Welch et al., 2016). Ideally, these controlled feedings may occur over the course of an animal's life (McCue, Amaya, et al., 2013; McCue, Guzman, Passement, & Davidowitz, 2015), but should at least include a biologically relevant period (e.g. hours and days for plasma and liver vs. weeks and months for muscle and connective tissue) that is sufficient to permit measurable enrichment of endogenous tissues (Khalilieh, McCue, & Pinshow, 2015; McCue, Arquisola, et al., 2013; Munoz-Garcia, Aamidor, McCue, McWilliams, & Pinshow, 2012).

In practice, diets that are supplemented with certain ^{13}C-labelled amino acids will gradually enrich the body proteins. Essential amino acids are preferred for this purpose because they are less likely than non-essential amino acids to be immediately oxidized upon ingestion (Berthold et al., 1991; McCue, Sivan, McWilliams, & Pinshow, 2010). Diets supplemented with ^{13}C-labelled fatty acids will isotopically enrich the body lipids. Essential fatty acids (e.g. arachidonic acid, linolenic acid, etc.) are not particularly useful for this approach because they can be prohibitively expensive and only account for a small proportion of the total body lipids (e.g. Ben-Hamo, McCue, Khozin-Goldberg, McWilliams, & Pinshow, 2013; Holmstrup, Hedlund, & Boriss, 2002; McCue, 2008; Mustonen et al., 2013). Common non-essential fatty acids (e.g. oleic acid, palmitic acid) are sufficient to cause measurable enrichment of the body lipids over time. ^{13}C-Glucose has been used to enrich hepatic and/or muscular glycogen stores (Gay, Schneiter, et al., 1994; Gay, Schutz, et al., 1994; Muller et al., 1997; Tanis et al., 1998; Tanis, Rietveld, Wattimena, Berg, & Swart, 2003). However, because animals can readily interconvert the carbon atoms of dietary glucose into both non-essential amino and fatty acids, it can be problematic to quantitatively interpret the experimental outcomes (McCue, 2013).

Otherwise identical populations of these artificially ^{13}C-protein-enriched or ^{13}C-lipid-enriched animals can then be exposed to resource (e.g. food or water) limitation and changes in their rates of endogenous nutrient oxidation can be compared over time within and across species (Figure 1d). This experimental approach has revealed that insects from different taxonomic orders vary widely in how they mobilize their finite lipid and protein resources (McCue, Guzman, et al., 2015). This approach has also been used to show that quail starving for several days oxidize stored lipids at a relatively constant rate yet exhibit large diel fluctuations in their rates of protein oxidation – a pattern that markedly differs from the typical mammalian response (McCue, Amaya, et al., 2013). We are not aware of this experimental approach being used yet to explore the fundamental rules that govern resource use between competing native and invasive animal species, but studies using artificially enriched tracers in plants have revealed important physiological differences during resource limitation (see below).

4.3 | Reproduction

Survival alone does not ensure the successful establishment of an invasive species; invaders also need to reproduce. It has been suggested that some invasive species benefit from allocating a greater proportion of their energy resources towards reproduction (Lambrecht-McDowell & Radosevich, 2005; Mason, Cooke, Moles, & Leishman, 2008; Morris, Walck, & Hidayati, 2002). SIA can be used to measure these vertical transfers (i.e. from parents to offspring) of nutrients (Figure 1b). In fact, previous studies of animals switched between C_3- and C_4-plant-based diets have permitted researchers to observe the vertical transfer of bulk nutrients into eggs (O'Brien, Fogel, & Boggs, 2002; O'Brien, Schrag, & Martinez del Rio, 2000) and milk (Boutton, Tyrrell, Patterson, Varga, & Klein, 1988; Chevalier, Pelletier, & Gagnon, 1984; Doronin, Bednik, Ivanov, Golichenkova, & Kalistratova, 2012; Metges, Kempe, &

Schmidt, 1990). We are unaware of studies comparing patterns of resource allocation towards reproduction between native and invasive animals.

Stable isotope analysis can be used to reveal where an animal exists along the continuum of capital-income breeding strategies (Boggs & Niitepold, 2014; Inger & Bearhop, 2008; Van Dyke & Beaupre, 2012). In practice, this involves providing isotopically labelled nutrients to a parental generation and recovering the tracers in the eggs or offspring. ^{15}N-tracers fed to several species of snakes during vitellogenesis showed that they varied widely in their reliance on income resources (Van Dyke, Beaupre, & Kreider, 2012). This experimental approach also revealed that flesh flies used stored (i.e. capital) resources for their first clutches of eggs but used recently ingested (i.e. income) resources for their second clutch (Wessels, Jordan, & Hahn, 2010); no such differences were observed in lizards (Warner, Bonnet, Hobson, & Shine, 2008). In related tests of nutrient transfer ^{15}N-labelled aphids were fed to predatory insects and spiders (Nienstedt & Poehling, 2000, 2004).

If individual classes of macromolecules are isotopically labelled, then researchers can make even finer distinctions about the vertical transfer of nutrients. Two studies used this approach to demonstrate that both lizards (Warner et al., 2008) and ducks (De Vink, Slattery, Clark, Alisauskas, & Hobson, 2011) provisioned eggs with proteins from recently ingested meals. In contrast, the egg lipids were derived exclusively from stored resources. Another study documented tradeoffs between allocation of dietary proteins to reproduction and wound-healing in lizards (Durso & French, 2017). Native gray-headed sparrows infected with malaria showed a similar trade-off in protein allocation, but invasive house sparrows showed no such pattern (Coon, Brace, McWilliams, McCue, & Martin, 2014).

5 | PLANTS AND SOILS

The success of many plant invaders hinges on their capacity to extract resources from the environment at greater rates or efficiencies than native species. Such resources are then allocated to structures (e.g. seeds) or processes (e.g. prolonged flowering), which likely further improve the success of the invasive plants. In nutrient-limited ecosystems, even small differences in efficiency of resource acquisition may become important, owing to the energy and carbon costs involved under these conditions.

5.1 | Water sourcing and water use efficiency

Water is the most limiting non-mineral resource for terrestrial plant distribution, but its abundance can vary across time and space. SIA can also be used to determine invasive plants' water use efficiencies (Seibt, Rajabi, Griffiths, & Berry, 2008) and explore the long-term behaviours of plant stomata during seasonal

cycles. This method relies on the fact that the major CO_2-fixing enzyme for photosynthesis, Rubisco, has a higher affinity for the more abundant $^{12}CO_2$ molecule, compared to the scarcer, less common $^{13}CO_2$. During water limitation, there is usually an associated reduction in stomatal conductance. Consequently, the internal, sub-stomatal CO_2 concentration becomes reduced in leaves. Since Rubisco would first favor the fixation of the lighter $^{12}CO_2$ molecules, the ^{12}C:^{13}C ratio gradually declines owing to less discrimination against the available $^{13}CO_2$.

The lower discrimination values are driven by stomatal closure and/or a higher photosynthetic water use efficiency (WUE) (Richards, 1996; Werner et al., 2012). Measures of WUE indicate how much CO_2 is fixed per unit of water lost via the leaf stomata. Using $\delta^{13}C$ allows comparison of water relations in invasive and native plants over long periods or during a specific growing season (Figure 1e). This would indicate the capacity of invasive plants to acquire and use water efficiently, and can provide further insights into the ability of the invasive species to survive water limitations (Werner et al., 2012).

Stratton and Goldstein (2001) cautioned that care should be taken when using ^{13}C values as indicators of long-term or integrated WUE, because the ^{13}C values may be incorrectly interpreted when the species' leaf production is not taken into account. In their study, the ^{13}C values of the invasive Brazilian peppertree and six native Hawaiian tree species showed that the rapid growth of the invasive tree is due to its greater ability to deal with variation in water availability, but that the seasonal leaf expansion of the species greatly affected the ^{13}C values (Stratton & Goldstein, 2001).

Researchers have used $\delta^{13}C$ values to compare WUE over two seasons between invasive gamba grass *Andropogon gayanus* and a native grass in Australia. Both C_4 grasses had similar WUE during the wet rainy season. However, during the dry season, the native grass senesces while gamba grass showed higher WUE compared to the wet season (Ens, Hutley, Rossiter-Ranchor, Douglas, & Setterfield, 2015). This physiological plasticity has probably contributed to the invasiveness of gamba grass in Australia.

Invasive plants often have major impacts on water resources throughout an ecosystem and SIA can be used to investigate these (Antunes, Diaz-Barradas, Zunzunegui, Vieira, & Maguas, 2017). Researchers measured the ^{18}O in xylem water and used a mixing model to partition the contribution of precipitation versus ground water in invasive acacia in Europe and showed that the species exhibits large seasonally plastic responses (Maguas et al., 2011). A similar approach was used to document water sourcing in invasive trees in Sudan and USA (Saito et al., 2014). Both studies suggested that the increased capacity for the invasive to adapt to changing water sources may provide competitive advantage over natives.

5.2 | Soil carbon and microbial communities

Stable isotope analysis has utility in elucidating trophic relationships in hidden biodiversity compartments, where other approaches are

difficult to apply. For example, in the past two decades, SIA has revolutionized our understanding of soil food webs which are critical to the functioning of terrestrial ecosystems (Potapov, Tiunov, & Scheu, 2019). It was revealed that these webs are based primarily on microbial resources and not dead plant material, and that different taxonomic groups of microbes are linked into different pools of organic carbon in the soil. For example, an invasive Australian acacia was recently shown to decrease the ^{13}C of organic matter in the soil (Ulm, Jacinto, Cruz, & Maguas, 2017), but the role of microbes in this response is not fully understood.

The potentially profound impacts of below- and above-ground invasions on soil communities have been studied using SIA. In an interesting application of SIA to below-ground dynamics, researchers showed that the noxious spotted knapweed parasitizes carbon from native grass species via below-ground mycorrhizal networks. This mechanism may contribute to the wholesale competitive exclusion of natives, a common feature of perennial plant invasions (Carey, Marler, & Calloay, 2004).

Invasive species, especially plants, can have pronounced impacts on the microbial components of the environments they invade. Dense stands of invasive plants can alter soil nutrient loads through root exudates and inputs via leaf litter which in turn affect soil nutrient status and the functionality, diversity and structure of soil microbial communities (Hu et al., 2018; Waring et al., 2015). These soil microbial communities play an important role in the biogeochemical cycling of soil elements; invader-induced changes in the abundance and composition of microbial communities thus represent a significant ecological impact (e.g. Yang, Jeelani, Leng, Cheng, & An, 2016). Despite their importance and vast diversity, the taxonomic identity of microbes involved in specific processes has historically been confined to the small fraction of culturable organisms. While this has changed with the advent of high-throughput next-generation sequencing (NGS) approaches, comparable advances in determining microbial functionality is still lagging. SIA may provide opportunities to overcome this limitation.

Stable-isotope probing (SIP) is a technique developed to trace nutrient fluxes during biogeochemical cycling by microbes. When microbial communities are exposed to (fed) substrates enriched with heavier stable isotopes those taxa that incorporate them can be separated from those containing lighter isotopes through isopycnic centrifugation (Radajewski, Ineson, Parekh, & Murrell, 2000). DNA isolated from the heavier isotope of microorganisms can then be characterized taxonomically using traditional NGS analysis (e.g. 16S rDNA gene metabarcoding). In practice, SIP has been used to show that only a subset of rhizosphere microbiomes metabolize photosynthetically derived carbon in various crop plants (Haichar et al., 2008). This was done by allowing plants to fix artificially enriched $^{13}CO_2$ into their tissues, followed by tracking of $^{13}CO_2$ into soil microbial biomass (Haichar et al., 2008). Using a similar approach researchers treated coastal mudflats with ^{13}C-labelled methane and determined that net methanotrophic activities were attenuated in areas where alien plants were present (Deng et al., 2019). SIP may hold promising future research directions in invasion science. For example, providing microbial communities of neighbouring invaded and uninvaded habitats with isotope-enriched substrates may not only provide key insights into how invasive species impact microbial community diversity but also function.

5.3 | Nitrogen fixation and nitrogen uptake

The use of SIA is not limited to water and carbon relations and can also be applied to the acquisition of nitrogen, especially by invasive legumes which indirectly fix atmospheric N_2 (Ulm, Hellmann, Cruz, & Maguas, 2016; Werner, Zumkier, Beyschlag, & Maguas, 2010). Invasive plants in nutrient-limited ecosystems are often legumes (Paynter et al., 2003). Most legumes form symbioses with bacteria, known as rhizobia, which can acquire N_2 gas from the atmosphere via biological nitrogen fixation (BNF). Rhizobia fix nitrogen through nitrogenase activity that reduces atmospheric N_2 to ammonia. Nitrogenase preferentially incorporates the lighter isotopes of atmospheric N_2 (Unkovich, 2013). Measures of δ^{15}N can therefore be used to determine the contribution of BNF to the N budget of these invasive legumes (Figure 1c). With careful experimental planning and analyses, the efficiency of BNF can be calculated for these legumes in nutrient-limited soils (Magadlela, Beukes, Venter, Steenkamp, & Valentine, 2017; Magadlela, Perez-Fernandez, Kleinert, Dreyer, & Valentine, 2016).

It is of great importance to the survival of the invasive plants, not only to be able to acquire N from both soil and atmospheric source, but to do so efficiently. For example, across 19 non-native Australian *acacia* species with varying levels of invasiveness in nutrient-poor soils of South Africa's fynbos vegetation, invasion success (in terms of geographic spread of invasive populations) was unrelated to N-fixation efficiency (determined using δ^{15}N signatures) as all species fixed N equally efficiently (Keet, Ellis, Hui, & Roux, 2017). In other studies of N-uptake, researchers injected the soil with a $^{15}NH_4$ tracer to investigate intraspecific and interspecific competition and determined that invasive acacias somehow reduced the ability of native plants to take up nitrogen (Werner et al., 2010) or otherwise outcompeted the native plants for available nitrogen (Peperkorn, Werner, & Beyschlag, 2005).

Over time, invasive legumes tend to enrich soils with nutrients, especially nitrogen. This process may lead to indirect impacts on above- and below-ground soil communities that resemble 'small-scale' isoscapes (Rascher et al., 2012). Again, SIA provides unique opportunities to investigate such local impacts. For example, researchers have examined the impacts of invasive long-leaved wattle in dune systems in Portugal (Hellmann, Werner, & Oldeland, 2016). Using foliar δ^{15}N isoscapes together with nitrogen concentrations of co-occurring native species, they found the native species to have a more than twofold increase in foliar N and a δ^{15}N enrichment of up to 8‰, when growing near the invasive species. Depending on the native species, the foliar ^{15}N values can either be increased or decreased by the presence of long-leaved wattle (Hellmann et al., 2016).

SIA can also help researchers determine the spatial scales of ecosystem invasion impacts, such as altered nitrogen cycling. Community-scale native foliage $\delta^{15}N$ isoscapes have, for example, shown that the spatial dimension of changes associated with the invasion of an exotic N_2-fixing acacia species was much greater than the distribution of the invasive species itself (Rascher et al., 2012).

5.4 | Invasional meltdown

Invasive species can have profound impacts on critical ecosystem processes, such as carbon and nutrient cycling (D'Antonio & Vitousek, 1992; Simberloff, 2006). The system changes they drive can in turn favour their competitive dominance and spread via self-reinforcing positive feedback loops that might be a ubiquitous feature of successful invasions (Le Roux et al., 2017; Levine, Pachepsky, Kendall, Yelenik, & Lambers, 2006). Also of concern is the possibility that the impacts of one invasive species might increase the susceptibility of an ecosystem to further invasions, a phenomenon known as *invasional meltdown* (Simberloff & Von Holle, 1999). Invaders can facilitate subsequent invasions through several pathways, including impacts on ecosystem properties, direct nutritional links or habitat creation. SIA can be used to understand these pathways to invasional meltdown.

Invasion of Hawaiian woodlands by C_4 grasses has altered community composition and important ecosystem drivers, such as fire cycles, N-mineralization, and net primary productivity (Mack, D'Antonio, & Ley, 2001). Dominance of one invasive grass in the years after fire dramatically increased N-cycling rates. Increased N availability favored the N-limited invasive grass in a positive feedback loop further reinforcing its dominance. However, researchers found that this feedback loop has not persisted through time (Yelenik & D'Antonio, 2013). They used SIA to show that later-stage invaded soils have suffered loss of nitrogen through denitrification pathways and that long-term ecosystem N-depletion feeds back negatively on the dominance of invasive C_4 grasses.

Alteration of ecosystem processes such as nitrogen cycling can result in invasional meltdown if impacts of one invasive species facilitates invasion by others. Ecosystem state shifts are likely to persist after eradication of invaders (the so-called *legacy effects*) and complicate the process of restoring native communities at previously invaded (Yelenik & D'Antonio, 2013) or disturbed sites (Rascher, Grobe-Stoltenberg, Maguas, Meira-Neto, & Werner, 2011). In the C_4 grass example from Hawaii discussed above, for instance, the long-term ecosystem N-depletion under invasion does not favor native species re-establishment, but rather benefits invasive N-fixing trees (Yelenik & D'Antonio, 2013).

6 | PATHS FORWARD

Despite the popularity of SIA in specific areas of ecological research, its application in addressing pertinent questions in invasion biology

has only recently emerged. What makes some species successful invaders while others fail is a pivotal question that is attracting major research effort (e.g. Fournier, Penone, Pennino, & Courchamp, 2019). Despite major advances, much uncertainty remains, largely due to the high level of context dependency of invasions (i.e. introduction history (timing and pathways) and attributes of both invasive species and the invaded habitat must be considered) (Richardson & Pysek, 2006; Thuiller, Richardson, Rouget, Proches, & Wilson, 2006). This review makes it clear that SIA presents biologists with unprecedented and exciting opportunities to better understand many of the key processes and mechanisms that underlie successful biological invasions.

A recent horizon scanning analysis identified emerging scientific, technological, and sociopolitical issues that are likely to affect how biological invasions will be studied and managed over the next two decades (Ricciardi et al., 2017). SIA has great potential to contribute insights in most of the broad categories of topics identified in this exercise. For example, within the theme of biotechnological issues, changing agricultural practices were identified as a potential driver of major changes in the trajectories of invasions. New investments by commercial businesses are seeking to enhance production through the more effective use of soil bacteria and fungi. Such practices could trigger invasions by currently non-invasive crops or co-occurring plants but may also have substantial impacts on soil microbiomes. While new insights are emerging on the effects that some invasive plants have on soil microbiomes, our understanding of their magnitude is limited by the approaches available to evaluate them. Next-generation sequencing (NGS) has increased our capacity to understand soil diversity impacts (e.g. Kamutando et al., 2017), but often this approach lacks functionality (but see e.g. Jackson, Grey, Miller, Britton, & Donohue, 2016). Even diversity metrics derived from NGS are largely uninformative due to low taxonomic resolution. Although SIA cannot circumvent this issue, it can provide more precise information about functional changes in microbiomes, for example, using stable-isotope probing (SIP) approaches. Combining NGS, SIP, and soil microbial enzymatic analyses is a promising approach to better understand invader impacts on microbiomes.

Half of the emerging challenges and opportunities in invasion science identified by Ricciardi et al. (2017) were categorized as 'sociopolitical issues'; these are areas where human perceptions and values either complicate management options or potentially provide new opportunities for dealing with biological invasions. There are also clear opportunities for SIA to address key questions in such research areas. Conflicts of interest that thwart effective management of invasions often revolve around imperfect understanding of the impacts of invasive species (Woodford et al., 2016). A striking example is the debate around the impact of non-native trout in South Africa, where parties are calling for trout to be removed from the list of invasive species in national regulations. These parties argue that the impact of trout on native biodiversity is unsubstantiated and emphasize that many people derive pleasure and, in some cases, income from opportunities that trout provide for recreational fishing. Such conflicts of interest greatly complicate the management of this

species in South Africa and of many other invasive species worldwide (Woodford et al., 2016).

Many alien plants that were originally introduced to provide new ecosystem services or to supplement existing ecosystem services have become invasive. Conflicts of interest relating to the management of such species usually relate to perceptions and assumptions about various facets of resource use by the alien plant. Many studies have used SIA to characterize water use of alien trees in arid ecosystems and riparian habitats and to clarify the extent to which the alien species compete with native species for water (e.g. Busch & Smith, 1995). Isotope studies have been used to provide motivation for expensive management interventions – e.g. in the case of *Prosopis* invasions in the Northern Cape of South Africa where invasive stands use large volumes of groundwater (Dzikiti et al., 2013).

A clear objective of much research in invasion science is to inform efforts to restore habitats impacted by invasive species (e.g. Holmes, Richardson, Esler, Witkowski, & Fourie, 2005). The examples above demonstrate that SIA should be an important part of the toolbox required to understand the diverse impacts of invasions on, for example, food web structure and ecosystem functioning. Isotopes also have potential as a tool for monitoring the success of restoration efforts. For example, in conjunction with more traditional diversity-based approaches, SIA has been used to confirm that saltmarsh restoration attempts have been successful in re-establishing functioning native communities with food web structure and carbon cycling dynamics that closely approximate those of pre-invasion communities (Dibble, Pooler, & Meyerson, 2013; Kindscher & Tieszen, 1998). Analyzing isotopic signatures at different depths along soil cores potentially provides a means of temporally tracking ecosystem functions, such as carbon cycling, through the invasion–restoration trajectory, and for establishing pre-invasion baselines (Kindscher & Tieszen, 1998).

In conclusion, we propose that several concurrent, innovative advances in SIA tools and techniques, Such as increasing availability of high-resolution isotope landscape maps for diverse stable isotopes and a cheaper expanded range of artificial chemical enrichment products, are allowing key questions in invasion ecology to be answered with unprecedented resolution and precision. Tackling classic problems in ecology using SIA in both laboratory and field investigations promises to provide insight into the fundamental mechanisms underlying invasions and the impacts that invasive organisms may have on native species communities.

AUTHOR'S CONTRIBUTIONS

M.D.M., S.C.-T. and J.S.T. conceived project; All authors contributed to ideas, data collection and literature review; M.D.M. led the writing; M.D.M. and J.J.L.R. developed the graphical presentation; All authors contributed to writing of sections, edited and approved the final ms.

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DATA AVAILABILITY STATEMENT
There are no raw data for this paper.

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