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TRENDS IN AQUATIC ECOLOGY III

Review Paper

Invasion impacts on functions and services of aquatic ecosystems

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Abstract Non-native species can simultaneously affect ecological structures, functions, and services of the invaded ecosystem. In this paper, we report that the study of non-native species impacts on ecosystem function is an emerging topic in aquatic ecology, though studies measuring functions remain relatively uncommon. We hypothesized that study of ecosystem function can reveal emergent effects of non-native species when community structure appears to be unimpacted and the study of multiple functions has the potential to identify impacts masked by food-web complexity. We compiled information from Web of Science to create a pool of papers ($n = 199$) addressing ecosystem functions and services that we surveyed to evaluate our hypotheses. The number of publications referencing ecosystem function has increased since 2002, but only 10% of papers measured ecosystem functions as defined in our work. Additionally, 80% of publications reporting functional metrics addressed primary production and nutrient fluxes, while a low number of manuscripts (6%) directly linked the impact of non-native species on ecosystem functions to ecosystem services. We recommend future work focus on less-studied functions (e.g., bioturbation, decay rate, biomagnification), assess multiple functional metrics, link functions to services, and use networks to understand impacts from multiple dimensions of an invaders ecology.

Keywords Biogeochemistry · Ecological stoichiometry · Ecosystem function and structure · Energy web · Primary and secondary production

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Introduction

The spread of species outside of their native range has emerged as a global concern (Early et al., 2016). There are ample examples of non-native species altering aquatic ecosystems (marine, estuarine, and freshwater) at multiple ecological levels that could ultimately lead to long-term ecological and evolutionary changes

(Mooney & Cleland, 2001; Cucherousset & Olden, 2011; Havel et al., 2018). A large body of the literature has pointed out that the detrimental effects of established alien species on native species (e.g., extirpation of local populations, changes in diet, and hybridization) result in shifts of community composition and alteration of food-web structure (Vander Zanden et al., 1999; Olden et al., 2008; Harrison et al., 2013). Less commonly documented are changes caused by non-native species at the ecosystem level, including on ecosystem structure, function, and service (Figueredo & Giani, 2005; Cucherousset & Olden, 2011).

Ecologists use the terms ecosystem structure and ecosystem function in diverse ways in ecological publications (Jax, 2002; Electronic supplementary material 1). We use ecosystem structure as the biotic and physical composition of ecosystems characterized by metrics including relative abundance of species, the physio-chemical characteristics supporting them, and their arrangement in space and time (Myster, 2001). We follow Strayer (2012) in limiting ecosystem functions to the "processes that determine the amount, forms, distribution, fluxes, import and export of energy and various materials, including (but not limited to) carbon, macronutrients such as nitrogen and phosphorus, important trace materials, and toxins." Impacts by invaders on ecosystem structure are likely to also affect ecosystem function. For example, Huryn (1998) found that primary productivity in a stream with non-native trout was sixfold higher than in a stream where the trout were absent, in part because of strong top-down control that these fish exerted on community composition of primary consumers. Beavers (*Castor canadensis*) introduced in Chile modified riparian habitat to change streams to ponds with impacts on macroinvertebrate community structure and secondary productivity (Anderson & Rosemond, 2007). The non-native sailfin catfish, *Pterygoplichthys* spp., reduced primary productivity in a nutrient-limited river by consuming benthic algae (Capps et al., 2015a). With the increase in human migration and biotic exchange, the introduction of alien species is increasingly linked to losses of species with emergent effects on ecosystem structure and function (Sala et al., 2000).

A diversity of ecosystem functions and proxies of functions have been targeted for study in the context of biological invasions of aquatic ecosystems (Table 1). Primary and secondary production and nutrient turnover rates are the most studied ecosystem functions. Animals modifying their physical environment as ecosystem engineers is a common route for invasive species to impact ecosystem functions (Jax, 2002; Sanders et al., 2014). In aquatic ecosystems, bioturbation, whereby animals directly or indirectly affect sediment matrices by nest construction, sediment particle reworking, and burrow ventilation (Kristensen et al., 2012), is a widespread mechanism for ecosystem engineering. Biomagnification, by which xenobiotic substances are transferred and concentrated in food webs (Gray, 2002), is a process infrequently linked to invasive species impacts and ecosystem function, but with the potential to impact top trophic levels with implications for food-web function.

Invasion biology has focused on understanding and predicting invasion success with mixed results (Jeschke, 2014). Recent work has advanced theory from population and community processes to ecosystem function and services. For example, Dick et al. (2013) have suggested comparing functional responses of invasive and native taxa may have predictive power for invasion success and subsequent impacts on population dynamics. Through a meta-analysis, Gallardo et al. (2016) demonstrated that the effect size of an invader's impact on ecosystem structure and ecosystem function varies by trophic level, functional group, habitat, and physio-chemical variable measured. This work highlights how the response variable(s) measured can dramatically change the magnitude and direction of an invader's perceived impact. To understand an invader's net impact—all direct, indirect, and interactive effects—it is necessary to take a network approach, such as from structural equation modelling (Grace, 2006) and studying food webs (David et al., 2017). Doing so avoids misleading conclusions drawn from a relatively narrow breadth of the invader's potential impacts.

In this paper, we argue that study of impacts of invasive species on ecosystem function is an emerging topic in aquatic ecology. We propose that too few studies claiming to address functions or services (ecological functions directly linked to human values, Costanza et al., 1997) actually do. One reason for this gap may be that small direct impacts of a biological invasion have emergent effects on functions that are subtle or masked from direct observation. Ecosystem functions, such as rates of production or biogeochemical transformations, may impact one or more trophic

Table 1 Metrics used in studies of ecosystem function and units, only those with time measure ecosystem function by our definition

Ecosystem function	Units	Number of papers
Primary and secondary production with time	kg dry wt year^{-1}, g C m^{-2} year^{-1}, mg C m^{-1} d^{-1}, mmol m^{-2} h^{-1}, g m^{-1} year^{-1}, mg ash-free dry mass m^{-2} year^{-1}, kJ d^{-1} m^{-3}	7
Primary and secondary production without time	g m^{-2}, lbs, AFDM, AFDM m^{-2}, mg l^{-1}, %	12
Decomposition rate with time	Δ AFDM g d^{-1}, mol C m^{-2}, d^{-1}, mg d^{-1}	4
Decomposition (without time)	g dry wt	1
Biomagnification (without time)	mg kg^{-1}	1
Biomass flux	g m^{-2} d^{-1}	1
Biomass (without time)	g m^{-2}	1
Bioturbation (without time)	cm	2
Bioturbation rate	g m^{-2} h^{-1}	0
Nutrient cycling with time	mmol m^{-2} d^{-1}, mmol m^{-2} h^{-1}, mmol m^{-2} min^{-1},	11
Nutrient cycling without time	kiloton, kg m^{-2}, mg L^{-1}, %C, % N, C/N ratio, μg gDM^{-1}	5
Water clearance with time	Cells consumed ·10^{3} g^{-1} of mussel h^{-1}	1
Water clearance without time	m	1
Soil function without time	Soil quality index	1

The number of papers reporting the impact of non-native species on each metric in aquatic ecosystems in our literature search is listed. AFDM (Ash-free dry mass). Notes: The units of biomagnification refer to the total concentration of mercury (T-Hg); while "cm" in bioturbation is related to Surface Boundary Roughness (SBR). The unit of water clarity with no time refers to visibility distance (Secchi depth) and the "Soil Quality Index" is a proxy of soil function (e.g., resilience)

levels, entire food webs, and biogeochemical cycles. We support these assertions through a literature review. We also discuss extending theory about invasions beyond establishment and impacts on populations and communities and provide recommendations for study designs to test and develop that theory.

Methods

Literature review

We conducted a literature review using Web of Science (Clarivate Analytics) to compile a database of studies evaluating the impacts of invasive species on ecosystem functions in aquatic ecosystems. The search was conducted on June 1st, 2019, and included all years from 1926 to the date of the search.

The impact of invasive species on ecosystem function is an emerging topic in aquatic ecology

We began with general searches using combinations of the following search terms: invasive, non-native, exotic, alien, introduced, aquatic, marine, coastal, estuary, freshwater, lake, river, and stream. The most common terms from the literature were compiled to create structured and representative searches (Table 2). We used the results of this search to determine if the impacts of invasive species on ecosystem function can be considered an emerging topic in aquatic ecology. Emerging topic was defined as a topic that has been underrepresented in the literature until recently with a substantial increase in the number of publications in the last decade.

That literature search resulted in a large database that was filtered to identify studies focused on ecosystem function consistent with our definition. The resulting list of papers was long and contained many papers that did not quantify ecosystem functions. To ensure that our literature search represented

Table 2 A summary of the search terms used in conjunction with the list of species in Table 1 to find all relevant publications that fit into the corresponding categories

Category	Category description	Search terms
1	All publications that mention invasive species	(invasive* OR non-native* OR exotic*)
2	Publications that mention an ecosystem function or service	(invasive* OR non-native* OR exotic*) AND ("ecosystem function*" OR "ecosystem service*" OR productivity OR "energy" OR nutrient* OR "bioturbation" OR "biomagnification" OR biodiversity)
3	Publications that mention an ecosystem function or service AND use the terms ecosystem function or service	(invasive* OR non-native* OR exotic*) AND ("ecosystem function*" OR "ecosystem service*") AND (productivity OR "energy" OR nutrient* OR "bioturbation" OR "biomagnification" OR biodiversity)

the diversity of aquatic invasive species attracting research attention and a diversity of ecosystem functions, we compiled a list of widely studied taxa to explore in more detail (Table 3). We used this list of taxa to identify published works in one of three categories: (1) publications that address invasive species in any way; (2) publications within Category 1 that also address some kind of ecosystem function or service but do not necessarily use the terms "function" or "service"; and (3) publications within Category 2 that both address an ecosystem function or service and use the terms "ecosystem function" or "ecosystem service". Category 1 represents the growing body of invasive species literature, Category 2 represents the proportion of studies on invasive species that simply mention an ecosystem function or service, and Category 3 represents those studies that identify specific ecosystem functions and services. All search terms are summarized in Table 2. These literature searches were designed to be representative of all studies of aquatic invasive species, but we recognize that they exclude some species and terms, and thus our search results are intended to be representative rather than comprehensive.

The search terms for Category 3 yielded 199 publications, which we expected to be publications in Category 1 that were most likely to address ecosystem function or service quantitatively. We reviewed each publication in Category 3 to identify the ecosystem functions studied, which we recorded into a database (Electronic supplementary material 2) to facilitate our analyses and discussion.

Most studies claiming to address ecosystem function measure ecosystem structure

Ecosystem functions are dynamic processes that determine the amount, forms, distribution, fluxes, import and export of energy and various materials (Strayer, 2012). Therefore, documenting impacts of non-native species on ecosystem function requires the study of processes of ecological change (dynamics) measured as rates (through time) (Table 1). We hypothesized that most studies invoking ecosystem function are not measuring it, but assuming function based on effects of ecosystem structure and measured in static units. Describing the impact of non-natives on ecosystem function through measurement of rates (e.g., primary production g C m^{-2} $year^{-1}$) facilitates mechanistic understanding and enhances our ability to predict future structure and function of invaded ecosystems. We distinguished papers studying the rate of change of ecosystem parameters with time as part of the units from those without time in the units (an index of primary production such as the concentration of Chlorophyll a, Table 1). We considered research carried out through time, but failing to report rate or ecosystem function standardized per time unit, to be less useful to predict the long-term impact of non-natives at the ecosystem level because extra assumptions are required to create predictive models using those data.

Table 3 A list of all species included in the literature searches summarized in Table 2

Species	Common name	Type of animal	Literature search category		
			1	2	3
Channa spp	Snakehead	Fish	37	6	0
Siganus luridus	Dusky Spinefoot	Fish	29	13	0
Fistularia commersonii	Bluespotted Cornetfish	Fish	23	7	0
Siganus rivulattus	Marbled Spinefoot	Fish	18	8	0
Neopomacentrus cyanomos	Regal Demoiselle	Fish	4	0	0
Pempheris rhomboidea	Dusky Sweeper	Fish	1	0	0
Torquigener flavimaculosus	Yellowspotted puffer	Fish	1	0	0
Sargocentron rubrum	Redcoat	Fish	1	0	0
Pteragogus trispilus		Fish	1	0	0
Stephanolepis diasporas		Fish	0	0	0
Cerithium scabridum		Gastropod	3	0	0
Elodea canadensis	Canadian Pondweed	Plant	100	27	0
Sabella spallanzanii	Feather Duster Worm	Polycheate	20	4	0
Mysis relicta OR Mysis diluviana	Opossum Shrimp	Shrimp	64	19	0
Marsupenaeus japonicus	Japanese Tiger prawn		3	1	0
Tubastraea micranthus	Orange Cup Coral OR Sun Coral	Coral	25	5	1
Hemigrapsus sanguineus	Japanese Shore Crab	Crab	98	21	1
Neogobius melanostomus	Round Goby	Fish	495	83	1
Pterygoplichthys	Sailfin Catfish	Fish	58	17	1
Lates nilotica	Nile Perch	Fish	42	19	1
Diadema setosum		Sea urchin	3	18	1
Trachemys scripta elegans	Red-eared Slider	Turtle	103	20	1
Tapes philippinarum	Manila Clam	Bivalve	69	19	2
Petromyzon marinus	Sea Lamprey	Fish	178	26	2
Hypophthalmichthys nobilis	Bighead Carp	Fish	143	24	2
Ctenopharyngodon idella	Grass Carp	Fish	134	14	2
Esox lucius	Northern Pike	Fish	105	23	2
Tubastraea coccinea	Orange Cup Coral OR Sun Coral	Coral	51	13	3
Carcinus maenas	European Green crab	Crab	347	40	3
Mnemiopsis leidyi	Warty Comb Jelly OR Sea Walnut	Ctenophore	151	28	3
Pterois	Lionfish	Fish	286	44	3
Hypophthalmichthys molitrix	Silver Carp	Fish	234	33	3
Myriophyllum spicatum	Eurasian Watermilfoil	Plant	292	69	3
Eriocheir sinensis	Chinese Mitten Crab	Crab	110	19	4
Oncorhynchus mykiss	Rainbow Trout	Fish	767	120	4
Salmo trutta	Brown Trout	Fish	443	82	4
Cichlidae	cichlid*	Fish	260	50	4
Eichhornia crassipes	Water Hyacinth	Plant	266	122	4
Lagarosiphon major	African Elodea OR Curly Waterweed	Plant	47	15	4
Potamopyrgus antipodarum	New Zealand Mudsnail	Snail	145	26	4
Hydrilla	Water Thyme	Plant	249	62	5
Caulerpa taxifolia	Caulerpa taxifolia	Algae	297	66	7
Castor canadensis	beaver	Mammal	122	32	7

Table 3 continued

Species	Common name	Type of animal	Literature search category		
			1	2	3
Undaria pinnatifida	Wakame	Algae	149	41	8
Crassostrea gigas	Pacific Oyster	Bivalve	356	67	10
Cyprinus carpio	Common Carp	Fish	536	123	10
Oreochromis	tilapia	Fish	378	105	10
Marenzelleria		Polychaete	50	32	10
Orconectes rusticus	Rusty Crayfish	Crayfish	229	65	11
Procambarus leniusculus	Signal Crayfish	Crayfish	137	26	12
Corbicula fluminea	Asian Clam	Bivalve	316	93	14
Procambarus clarkii	Red Swamp Crayfish	Crayfish	469	123	18
Spartina alterniflora	Smooth Cordgrass	Plant	561	153	30
Dreissena polymorpha	Zebra Mussel	Bivalve	1011	310	31
		Total	8,353	1,868	199

The total number of search results returned in each Category identified in Table 2 are shown in the Lit. Search Category columns

Small direct impacts on native species may translate to large impacts on ecosystem function

We sought to quantify studies that documented invader impact on multiple ecosystem functions to explore their net impact across all ecosystem functions. To accomplish this, we determined the percentage of papers in Category 3 that measured impacts on multiple ecosystem functions. We also documented the percentage of papers that attempted to combine multiple functions to calculate a net impact on ecosystem function.

Impacts on ecosystem services are a subset of impacts on ecosystem functions

From the perspective of wildlife and natural resource managers, it is beneficial for studies to address the impacts of invasive species on ecosystem services (Costanza et al., 1997; Guerry et al., 2015). To study impacts on ecosystem services, papers were identified that link an impact to human values, the response variables that were addressed in each publication, and if those response variables referred to as an ecosystem function or service according to our definitions of ecosystem function and ecosystem service.

Results and discussion

The impact of invasive species on ecosystem function is an emerging topic in aquatic ecology

Our literature search returned 8,353 publications that mentioned invasive species (Category 1; Table 3, Fig. 1). Publications in Category 1 were published between 1966 and 2018 (results from 2019 were omitted for this tabulation because the year was not complete). Publications on invasive species started to increase in frequency in the early 1990s, reaching a maximum of 756 publications in 2018, the final year of this summary. A search of publications that mention ecosystem function or service (Category 2) returned 1,868 publications, with the earliest entry in 1990 and a similar increase in frequency as Category 1, increasing steadily from 2002 until reaching a maximum of 215 publications in 2018. Of those 1,868, only 199 mentioned both ecosystem function or service and one of the terms associated with function (Category 3). The earliest entry in Category 3 was in 2003, and papers in this Category have slowly increased to a maximum of 33 publications in 2018.

Not only has the number of publications in all three categories increased in recent years, but also the proportion of publications in Category 2 and 3 (Fig. 2). Category 2 increased from less than 10% of papers in Category 1 published in 1995 to over 25% in

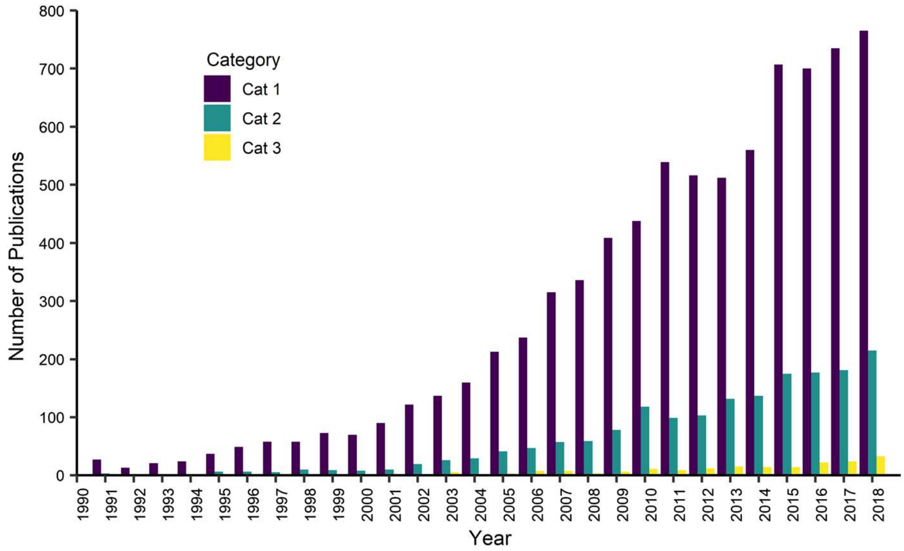

Fig. 1 Frequency of publications by year in categories 1, 2, and 3. Category (1) Publications that address invasive species in any way; (2) Publications within Category 1 that also address some kind of ecosystem function or service but do not necessarily use the terms "function" or "service"; and (3) publications within Category 2 that both address an ecosystem function or service and use the terms "ecosystem function" or "ecosystem service"

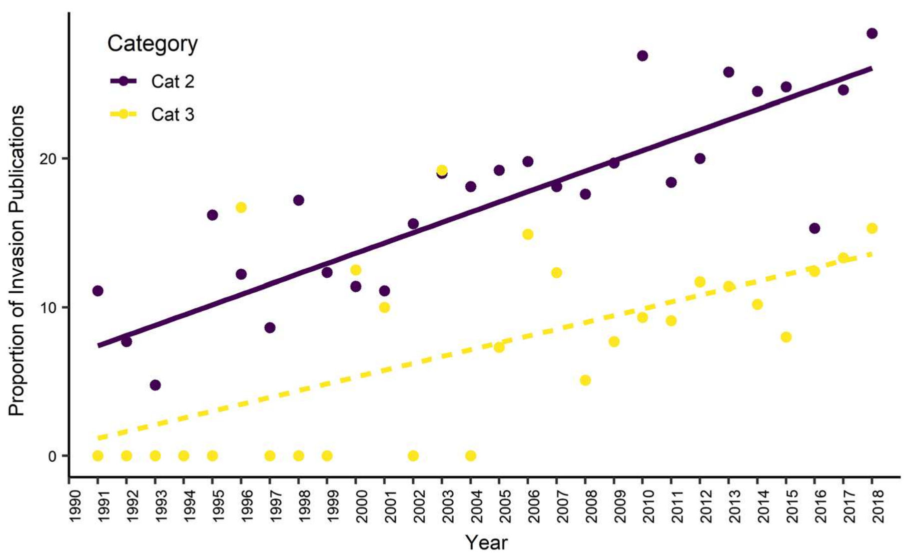

Fig. 2 The percentage publications by year that Category 2 and 3 make up of those in Category 1

2018. The number of Category 3 papers increased from 5% of papers in Category 1 during 2005 to over 10% in 2018. While the number of papers on invasion ecology also increased over this timeframe, the two-fold increase in the proportion of invasion papers studying impacts on ecosystem function or service (Category 3), relative to the number of papers on invasion (Category 1), demonstrates that the study of invasion impacts on ecosystem function and service is an emerging topic in aquatic ecology.

There has been a disparity in the efforts to document invasive-species impacts on ecosystem function between marine and freshwater systems, among ecosystem types, and among geographic regions (Fig. 3). Studies of freshwater systems (92 publications) outnumber those in marine systems (72 publications; Fig. 3A). The three most abundant ecosystem types in our search results were freshwater ecosystems: lakes (33 publications), rivers (27 publications), and streams (19 publications) (Fig. 3B). Four of the five least studied ecosystems were marine, including prominent ecosystems such as coral reefs and seagrass beds (Fig. 3B). Anthropogenic habitats, a canal (Kemp et al., 2018) and an aquaculture park (Lima et al., 2018), were targeted in only two publications. Most publications in this review came from Europe (57) and North America (45); Africa (6), Australasia (6), and the Caribbean (2) were the least studied regions (Fig. 3B). Future study of impacts from invaders on ecosystem function is needed in understudied areas that include some well-documented invaders, such as Caribbean coral reefs invaded by Lionfish (O'Farrell et al., 2014), Lake Victoria invaded by Nile Perch, *Lates niloticus* (Taabu-Munyaho et al., 2016), and New Zealand coastal marine habitats invaded by the seaweed Wakame, *Undaria pinnatifida* (Tait et al., 2015).

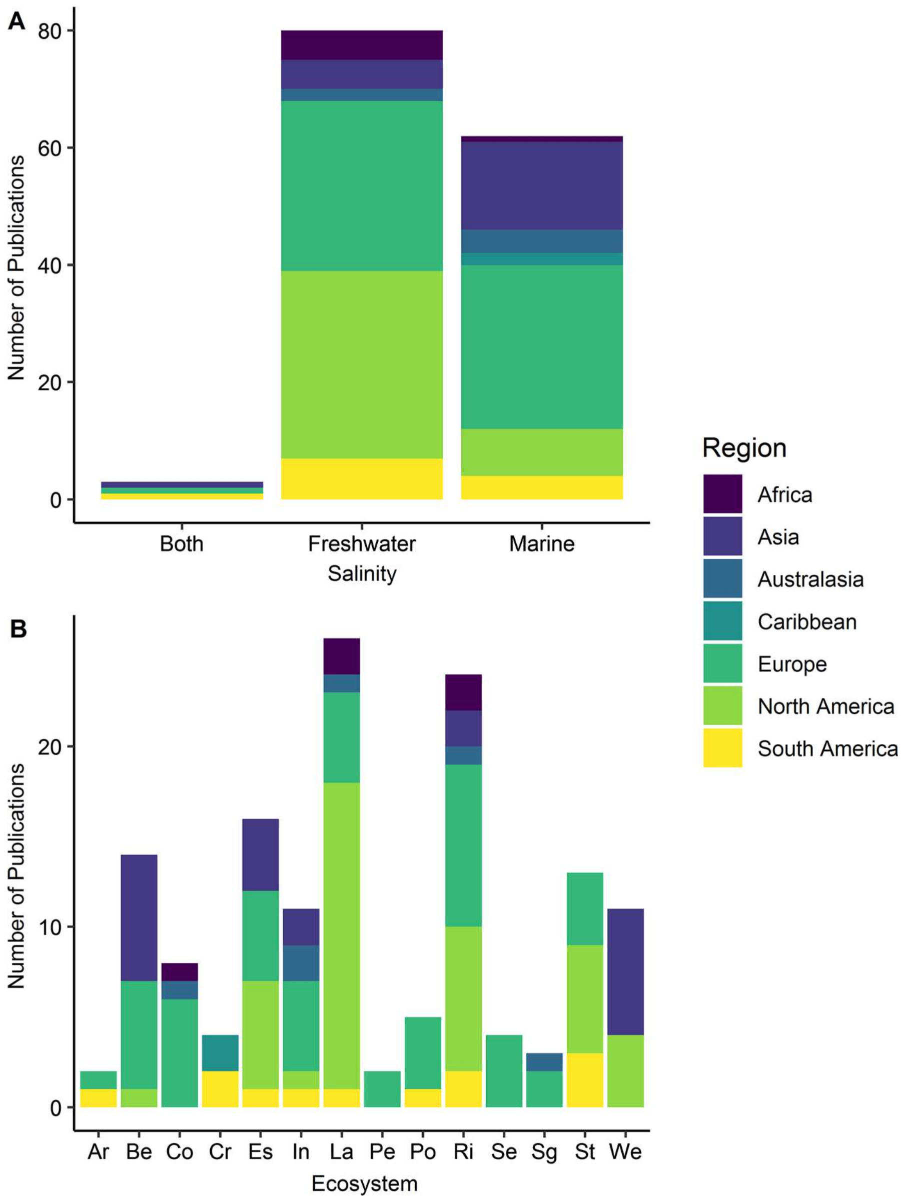

Fig. 3 The number of publications in Category 3 which were relevant to the literature review in each Category color-coded by region. **A** The number of publications from each salinity level. **B** The number of publications in each ecosystem (*Ar* artificial, *Be* benthos, *Co* coastal, *Cr* coral reef, *Es* estuary, *In* intertidal zone, *La* lake, *Pe* pelagic, *Po* pond, *Ri* river, *Se* sea, *Sg* seagrass, *St* stream, *We* wetland)

Ecosystem functions related to production, especially primary production, have received the most attention by researchers. The vast majority ($\sim$ 80%) of studies dealing with invasive species and their influence on ecosystem functions focused on ecosystem production (primary and secondary production, 40%) and nutrient cycling (40%) (Fig. 3A). Recent (after 2011) studies have documented impacts on biomagnification, bioturbation (Crespo et al., 2018), and biomass flux (Gergs et al., 2014). The relatively low proportions of publications on certain ecosystem functions [decomposition rate (11%), bioturbation (5%), water clearance rate (5%), and biomagnification (2%)] indicate the need for future work. For example, non-native fish can shift the nutrient balance within aquatic systems by increasing the amount of nitrogen (N) and phosphorus (P) entering the ecosystem via excretion (Schindler et al., 2001; Leavitt et al., 2008; Capps et al., 2015b). Fish excretion has been shown to mediate the flux of P from the benthos to the water column, a process that does not necessarily occur in the absence of these invasive fish (Schindler et al., 2001; Wahl et al., 2011; Capps & Flecker, 2013). Bivalves, fish, and vascular plants have received the most attention for their impacts as invasive taxa (Fig. 4B). Fish have the most diverse impacts on ecosystem function (4 functions), followed by bivalves and crustaceans (3 functions each). These differences may have more to do with a focus on high-profile invaders (e.g., zebra mussels and salmonids) than variation among taxa for the risk of impacts on ecosystem functions. The increasing attention to the impacts of invasive species on ecosystem functions and services has begun to provide a more comprehensive understanding of how these invaders should be managed. However, a clear gap in current knowledge indicated by our results is the potential for invaders to impact understudied ecosystem functions such as biomagnification, mediation of sediment, and water biogeochemistry by processes such as bioturbation, water clearance/filtering rates, and energy flow.

Most studies claiming to address ecosystem function measure ecosystem structure

Our review revealed that ecologists commonly invoke ecosystem function when discussing and drawing conclusions about their work without measuring function. In their seminal paper on documentation of impacts of invasive species, Parker et al. (1999) identified three types of impacts of invasive species on ecosystem function: (1) resource pools and supply rates; (2) rates of resource acquisition by plants and animals; and (3) disturbance regimes. By our definition, only the first two of these are ecosystem functions; we characterize disturbance regimes as part of ecosystem structure. Thus, we believe that invasion biologists have conflated application, categorization, and discussion of structure and function from the outset. We believe that maturation of the field requires more precision of both terminology and hypotheses (Jeschke, 2014; Jeschke et al., 2014), in addition to research focused on quantifying impacts on ecosystem function and service.

Many reported ecosystem functions are proxies for ecosystem function, rather than the actual function. Using a proxy response variable for ecosystem function may overlook other key ecosystem processes (Rosenfeld, 2002). One such proxy is water clarity. Water clarity has been used as a proxy for a variety of ecosystem functions (such as bioturbation, nutrient cycling, and primary productivity) and is often measured in meters of visibility (Volta et al., 2013). Measuring changes in the depth of water clarity does not provide any information on the magnitude, direction, or rate of change to the underlying ecosystem functions. Moreover, measuring only a single ecosystem function could be misleading about the general state of ecosystem function (Gamfeldt et al., 2008).

Of all papers we reviewed, 25% (n = 49) evaluated the impact of non-native species on ecosystem function through time (Table 3). However, according to our definition, to measure ecosystem function, the response variable(s) must be recorded as a rate (per unit time) and only 20 of these papers ($\sim$ 10%) did. For instance, Zhao et al. (2015) quantified changes in standing biomass (kg m^{-2}) of *Spartina alterniflora* and changes in N sequestration (mg L^{-1}) over the course of their experiment. This experiment, like all experiments, occurred through time. As a result, they documented changes over time; however, time was omitted from the units reported. We consider reporting rates to be important to compare studies that occur over different lengths of time and to assess the relative magnitude of impacts from various invaders. Even in the ideal scenario for drawing conclusions about invasions (or for comparisons of studies in any field),

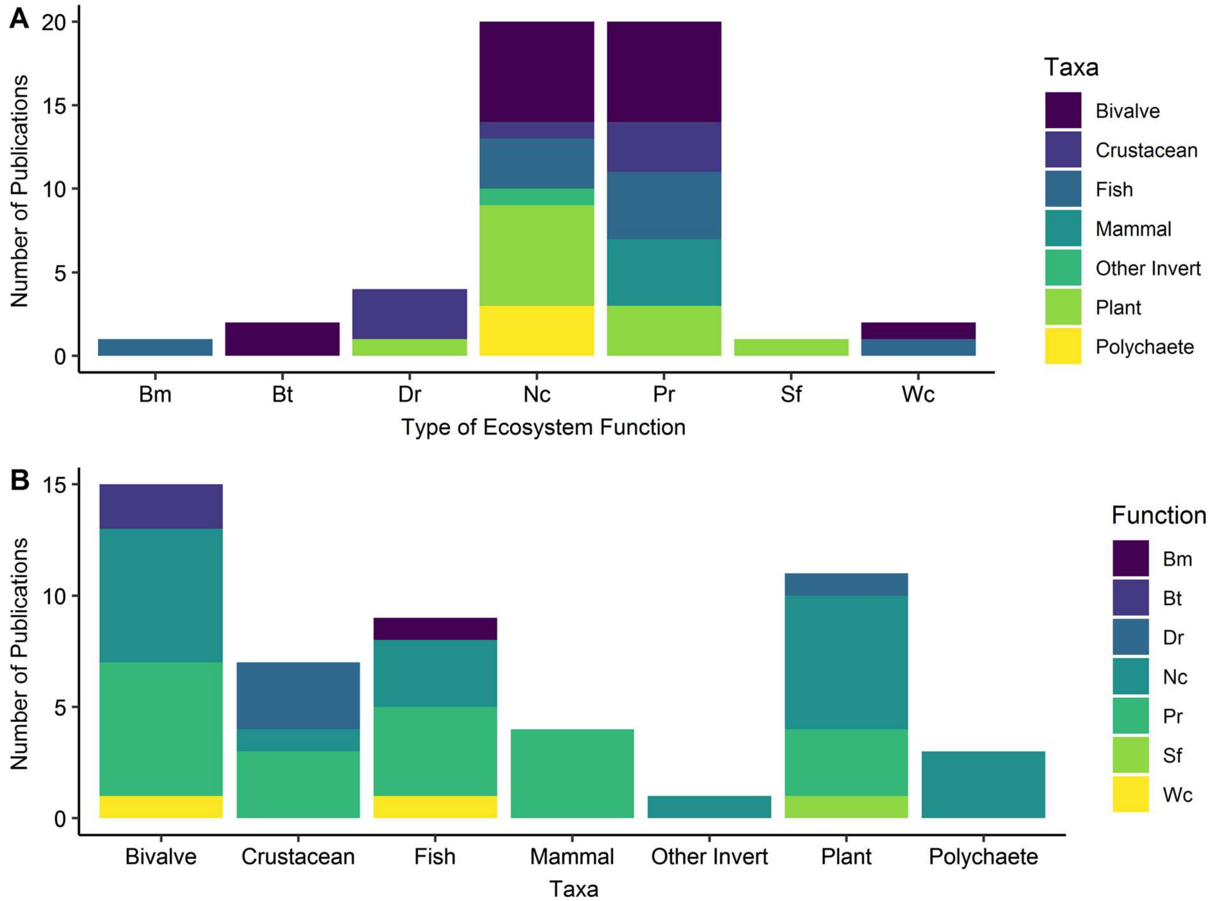

Fig. 4 The number of publications in Category 3 which studied ecosystem function, with or without time in the units, in each Category. **A** The number of publications on each type of ecosystem function color-coded by taxa. **B** The number of publications by taxa color-coded by the type of ecosystem function (*Bm* biomagnification, *Bt* bioturbation, *Dr* decay rate, *Nc* nutrient cycling, *Pr* primary and secondary production, *Sf* soil functioning, *Wc* water clearance)

when effect sizes are calculated and reported, if the response variables are not measured as rates, they may not be comparable. Knowing the magnitude of change without the rate of change leaves out important information for understanding invasion impacts and managing systems. A large magnitude of change over a long time interval has different ecological drivers and requires a different management response than a smaller magnitude of change over a short time interval. Reporting rates allows managers to assess which invaders require higher priority for resource allocation. For example, Doherty-Bone et al. (2018) reported litter decomposition rates (change in AFDM g day^{-1}) caused by non-native freshwater decapods (*Pacifastacus leniusculus* and *Eriocheir sinensis*) that were 50% higher than rates estimated for the native European crayfish (*Austropotamobius pallipes*). Similarly, Green et al. (2012) showed that the production of CO_2 (mg m^{-2} h^{-1}) increased 13-fold in areas heavily colonized by the invasive Pacific oyster (*Crassostrea gigas*). Both studies report the rate of change in ecosystem function, permitting comparisons among studies and among invaders to determine management strategies.

Another example of the importance of reporting rates is when considering invasion impacts are often subject to a lag effect (Simberloff, 2011). Is this lag effect greater for impacts on ecosystem functions and services? First, an invader must grow its population, displacing native populations and altering community structure, prior to having a high enough abundance to alter ecosystem functions, and thereby ecosystem services; a process that could take years. Do impacts by invaders on ecosystem function and service reach an equilibrium point? Do effect size and rate of impact vary over time post-invasion? These questions represent testable hypotheses. Studies testing them are needed to advance invasion theory to encompass impacts on ecosystem functions and services and model effects in planning scenarios. In fact, one such study demonstrated trophic niche expansion post-invasion (Pettitt-Wade et al., 2015). This implies a change in both the effect size and the rate of impact over time through trophic interactions by an invader.

Small direct impacts on native species may translate to large impacts on ecosystem function

An invasive species that has a small direct impact on ecosystem structure may have a large impact on ecosystem function. Ecosystem functions emerge from direct and indirect impacts that accumulate across multiple dimensions of ecosystem function. Paine's (1992) classic studies of intertidal communities demonstrated the presence of a few strong biotic interactions, with most interactions having small effects. This conclusion has been supported repeatedly in the literature (Bascompte et al., 2005; Wootton & Emmerson, 2005; Rooney & Mccann, 2012). The preponderance of weak interactions is considered a stabilizing force on community structure (Mccann et al., 1998; Emmerson & Yearsley, 2004; Rooney & Mccann, 2012). We hypothesize that invasive species yielding no strong direct interactions may have large impacts on ecosystem functions because of their effects through a diversity of weak biotic interactions, such as biotic effects on biogeochemistry (e.g., for ecosystem engineering see Jones et al., 1994; Sanders et al., 2014).

Of the 49 papers from Category 3 that met our criteria for ecosystem function, only 9 (18%) reported an invader's impact on multiple ecosystem functions. There were no studies in Category 3 that attempted to evaluate net impacts quantitatively across multiple ecosystem functions. Studies looking at a range of ecosystem functions are more likely to observe a strong impact or one mediated through more than one niche dimension. When focusing on a single dimension (e.g., a shift of trophic level caused by an invasive species, Fera et al., 2017) or organizational level (i.e., species–species comparison, Moreira et al., 2016) the conclusion could incorrectly be no impact by the invaders when there is an impact on a different ecosystem function or combination of functions. An example of this may be from Lionfish (*Pterois volitans* and *P. miles*) that have invaded Caribbean reefs. Benkwitt (2016) found Lionfish to have no impact on native fish density for both prey species and potential competitors. While total fish density may not have changed, the relative abundance of individual taxa or functional groups may have. Lionfish have been shown to be direct competitors with the endangered Nassau Grouper, as well as having varying impacts on herbivores and planktivores depending on habitat type (O'Farrell et al., 2014). In an example from freshwater systems, changes in predation pressure on herbivores and planktivores caused by non-native salmonids (e.g., *Salmo trutta*, *Salvelinus fontinalis*) caused a trophic cascade altering primary production as a result of shifts in the relative abundance of basal consumers (Simon & Townsend, 2003; Townsend, 2003). This suggests that while Caribbean reefs with Lionfish may not have changed native fish density, these reefs may demonstrate changes in ecosystem function similar to those documented in systems with introduced salmonids. Therefore, the lack of a local species-specific impact at population or community levels does not prohibit impacts by an invader on ecosystem function.

To fully understand the impacts of an invader, we must quantify impacts in as many dimensions of the invader's niche within the invaded ecosystem as possible. If we conceptualize the niche as the n-dimensional hypervolume following Hutchinson (1958), then all n-dimensions of an invader's niche have the potential to impact ecosystem function. While the practical limitations of an infinitely expanding niche concept are well established, it illustrates a practical limitation to assessing invader impacts. An invader can only be classified as having no net impact after being evaluated over multiple niche dimensions vis à vis ecosystem functions (primary production, nutrient cycling, energy flow, etc.). The magnitude of impacts must be aggregated across multiple dimensions to yield the net impact on ecosystem function; only a sum of zero would show an invader to have no impact on ecosystem function. Our review found no papers that attempted to do this experimentally and identified no taxa where impacts were studied on a comprehensive set of ecosystem functions identified by this review (Fig. 3B). Synthesizing this amount of information is best suited to a review paper, such as the work by Simon and Townsend (2003) on non-native salmonids in Australasia.

We suggest designing multifaceted food-web studies to document cascading impacts of invasive species at multiple trophic levels (David et al., 2017). For example, predation effects can cascade and alter non-trophic aspects of ecosystem function such as primary production (Simon & Townsend, 2003). An invader enters a system having both direct and indirect effects on native populations and communities. This changes the community's interaction and connectance webs (Post, 2002) resulting in altered ecosystem structure (e.g., species richness, relative abundance, direct and indirect interspecific interactions). Structural changes to populations and communities can result in changes to ecosystem functions (Fig. 5). Altered ecosystem function is revealed by differences in standing stocks of nutrients and organisms, and the flux of these stocks is an ecosystem function. Ecological stoichiometry (Sterner & Elser, 2002) is an informative component to understanding invasion impacts. Nutrients and calories measure the same process using different currencies. Proportions of macromolecules within an organism are directly related to food quality, thus ecosystem energy flux, and can be reflected in measures of ecological stoichiometry. For example, an invader could lower the fitness of a native species through trait-mediated indirect impacts altering the foraging behavior of the native taxa to lower availability of high-quality food. Due to the low-quality food source, the native taxa stop storing fat and become lower quality food for their consumers, reducing the energy flux through their node in the food web. In this scenario, the invader is impacting multiple ecosystem functions (nutrient cycling, energy flux, etc.) and all these changes could be detected using ecological stoichiometry in the context of energy (food quality) and food webs. We are unaware of any study that measures all steps simultaneously to populate a network. Studies that link impacts of food-web structure and connectance to stoichiometry are needed to document impacts on nutrient cycles and structure to energy webs (Fig. 5).

The invasion impacts on ecosystem function and service by mid-level consumers require study using this approach. The impacts of higher trophic level predators (Zaret & Paine, 1971; Simon & Townsend, 2003) and primary consumers or producers (Wahl et al., 2011; Capps et al., 2015a; Tait et al., 2015) are

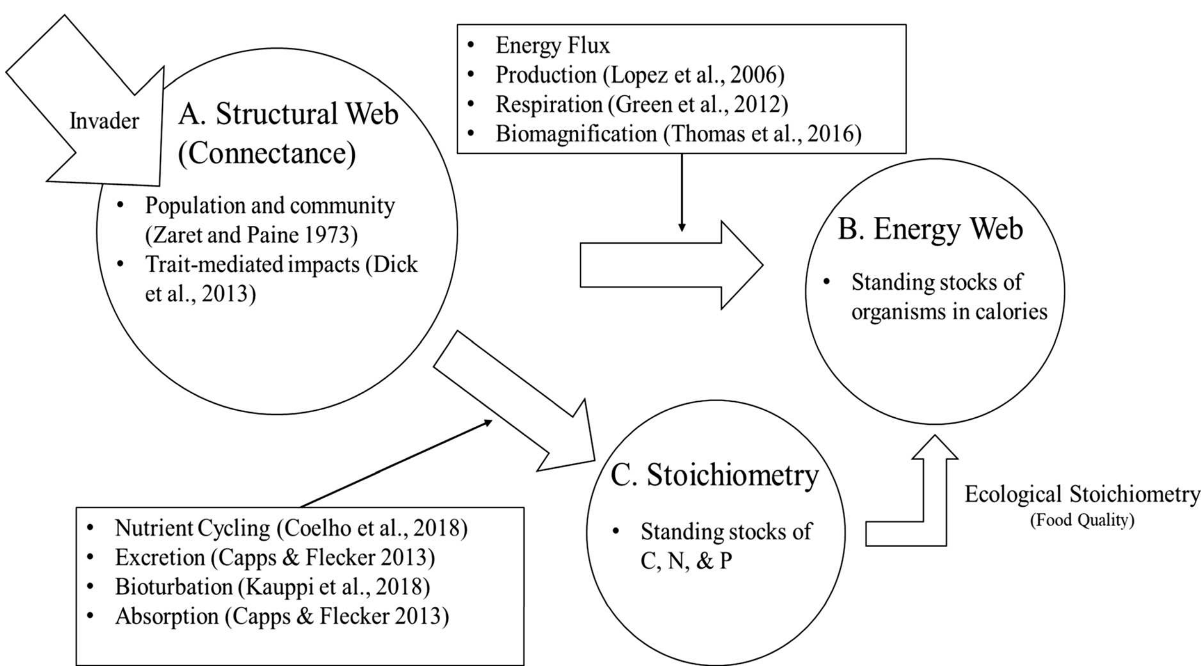

Fig. 5 Conceptual model of linkages of invader impacts on structural and connectance webs (**A**) to ecosystem attributes of energy webs (**B**) and stoichiometry (**C**). The rates at which these structures change are ecosystem functions. Ecological stoichiometry is the connection between ecosystem functions related to nutrient cycles and energy cycles, primarily through food quality

well documented. Mid-level consumers are under-represented in the literature (Fig. 4). Mid-trophic level consumers have a wide range of sizes, trophic positions, rapid response to environmental conditions, and high-numeric abundance, making them integral for understanding changes to food webs and the functioning of larger networks such as ecosystems (Stewart et al., 2017). Their nodes in the food web have more connections than nodes at the top or bottom, increasing the number of direct impacts they have. Top-down and bottom-up pressures emanate in one direction from the source's node. As a result of their position in the middle of the food web, mid-level consumers have multidirectional impacts (top-down, bottom-up, and lateral) through the ecosystem. The strength of a single interaction of a mid-level consumer may be weaker than that of a top predator or a primary producer, and the presence of many weak interactions can be a stabilizing force in an ecosystem (Rooney & Mccann, 2012). While a single interaction may not result in dramatic changes at any one level of community organization, those small changes have the potential to sum to large impacts on any given ecosystem function. We propose designing multi-faceted food-web studies linking food-web structure and connectance, energy flow, and ecological stoichiometry to document impacts on the underlying ecosystem functions (Fig. 5).

Impacts on ecosystem services are a subset of impacts on ecosystem functions

Only 6% of the reviewed publications addressed an ecosystem service, possibly indicating bias in our search terms toward those that address ecosystem functions. Most papers on ecosystem service ($n = 8$; 73%) also addressed ecosystem function. A publication that includes "ecosystem service" would only be included in Category 3 if it also included one of the terms associated with an ecosystem function. Therefore, most papers represented in Category 3 are those that studied ecosystem function and then translated those results into impacts on ecosystem services. When all aspects of ecosystem function are removed from the search terms, 138 publications on ecosystem services were returned. This contrasts with the 11 publications that were returned in Category 3 and exemplifies that studies rarely address ecosystem function and ecosystem services together.

Impacts on ecosystem services are often derived from multiple ecosystem functions, and the worth of those functions is translated to a monetary value that was not included in our search terms. For well-studied species such as the Zebra Mussel, understanding of ecosystem services is well underway with demonstrated impacts on water clarity (Limburg et al., 2010; Pejchar & Mooney, 2013), food production, and recreational activities (Pejchar & Mooney, 2013). These services are the result of ecosystem functions, including primary production, nutrient cycling, bioturbation, and energy flow (Limburg et al., 2010; Pejchar & Mooney, 2013). These examples show that assessing ecosystem services often follows a comprehensive understanding of changes in ecosystem function. As the understanding of impacts by invaders on ecosystem function continues to emerge, so too will the understanding of how those impacts on function translate to impacts on ecosystem services. Since ecosystem services often drive management decisions, it is equally important that translation from function to service carries with it the rates as a function of time so that reported values are comparable across disparate species and ecosystem functions. Although the link between function and service is often overlooked, it is needed for studies on ecosystem function to be communicated to various stakeholders and elicit appropriate responses in ecosystem management.

Conclusions and future work

In this paper, we demonstrated that the impact of non-native species on ecosystem functions and services is an emerging topic with increasing reference in publications over the last decade. However, most studies referencing ecosystem function measure invasive species impacts on community and ecosystem structure and reference the likely implications of these for function. We identified a relatively small number of papers measuring ecosystem function in the context of aquatic invasive species. Of these, primary productivity and nutrient fluxes are the most studied, while bioturbation, decomposition rate, energy flow, and biomagnification are under-represented in publications (Fig. 5). We found no studies that linked aquatic invasive species impacts on stoichiometry to energy flow. Future work should address the potential of non-native species on these and other ecosystem functions.

Perhaps unsurprising because of the relatively new focus on ecosystem function, we found few study systems where the impact of non-native species is traced in multiple dimensions and organizational levels. Papers dismissing the impact of non-native species on ecosystems based on study of a single or a limited number of dimensions of an invader's functional role may overlook real effects. We recommend caution when drawing conclusions from one-dimensional studies. Analysis of multiple ecosystem functions through food-web studies integrating connectance, structure, energy flow, and ecological stoichiometry have a greater opportunity to characterize emergent effects and yield a better understanding of net impacts (Fig. 5). We suggest designing studies with rates as response variables and reporting effect sizes to allow for accurate comparisons among studies. Given the importance of studying ecosystem services, we found a paucity of work addressing this topic. In both, marine and freshwater systems, linking non-native species influences on ecosystem functions to benefits that humans derive from ecosystems can improve the effectiveness of political supports for active and passive management and sustainability of natural capital.

Our review suggests that there are not enough data about the impacts of invaders on ecosystem function to test foundational theories in invasion ecology (Jeschke, 2014). For example, the biotic resistance hypothesis, also referred to as the diversity-invasibility hypothesis (Elton, 1958; Levine & D'Antonio, 1999; Jeschke, 2014; Jeschke et al., 2014), proposes that species-poor communities are more readily invaded than species-rich communities because of niche-packing and resource-use saturation. Do the same factors that influence invasion success influence the invader's impact on ecosystem function and service? Despite the lack of data, extrapolating this theory and others beyond the establishment of an invader to the invader's impact on ecosystem functions and services is possible. Do invaders that become established in more diverse systems have weaker impacts on ecosystem function as a result of the increased number of small, stabilizing interactions? Are the outcomes under this theory the same for invaders of different trophic levels and functional guilds? Expanding the biotic resistance hypothesis to ecosystem services, are invasions to more diverse systems more or less costly? These logical extensions to ecosystem function and service can be applied to most, if not all, existing hypotheses about invasion success. We believe that doing so will expand our understanding of invasive species impacts and social costs, and facilitate communication of these costs to the public.

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