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Review Article

Resource subsidies mediated by non-native species: a review

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Abstract

Non-native species are recognized as one of the major drivers of biodiversity change globally, with profound impacts on ecosystem functions and services. Despite the high number of studies on non-native species published, mainly in the last two decades, an often-overlooked aspect is their role as mediators of resource subsidies (the cross-boundary movement of energy, nutrients, or materials). This topic may have theoretical and empirical implications because non-native species may play a major role in ecosystem connectivity by transporting—or interrupting the transport of—energy and organic matter. Therefore, the main aims of this review were to (1) assess temporal trends, geographic distribution, and methodological approaches in research on resource subsidies mediated by non-native species; (2) synthesize how non-native species alter the magnitude, direction, and dynamics of resource subsidies across ecosystems and their implications for ecosystem functioning; and (3) identify key gaps in current knowledge and define future research priorities. The review retrieved 143 publications, resulting in 212 case studies, that collectively show that non-native species can both reduce and increase resource flows across ecosystem boundaries, with implications for ecosystem dynamics and connectivity. Although terrestrial and freshwater connectivity accounted for the majority of published case studies (56%), many ecosystem linkages remain underexplored. A significant geographic bias was found, with Africa being severely understudied (2.8% of all publications), followed by Asia (7.7% of all publications). Taxonomic representation was also skewed, with the majority of studies focusing on non-native plants (28.8% of case studies), non-native fish (25.5% of case studies), and mammals (21.7% of case studies), whereas fungi (0.9%) and bacteria (2.4%) were largely neglected despite their fundamental roles in decomposition processes. Key priorities for advancing this field include long-term monitoring, the application of emerging molecular and analytical tools (e.g., telemetry, eDNA, metabarcoding, and isotopic tracers), and the integration of artificial intelligence to synthesize large datasets. The findings provide the first synthesis of resource subsidies mediated by non-native species. This information is crucial for biodiversity conservation and the effective management of ecosystems and their connectivity.

Key words: biological invasions, connectivity, ecosystem functioning, management, meta-ecosystems, non-native species

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Introduction

Resource subsidies, defined as the cross-boundary movement of energy, nutrients, or materials, are central to ecosystem functioning (Polis et al. 1997). These resources, originating in one ecosystem and transported to another, can alter population and community dynamics, linking ecosystems through fluxes of organisms, energy, and matter (Gounand et al. 2018). Such flows can either enhance or suppress production, modify food webs, and shape species interactions across spatial scales (Subalusky and Post 2019). These transferred resources are also termed spatial subsidies or trophic subsidies (Polis et al. 1997), and the term resource subsidy is used throughout this review.

Despite the theoretical and management importance of resource subsidies for better understanding the roles of biodiversity and ecosystem functioning, terrestrial, freshwater, and marine ecosystems have largely been studied separately, probably because of the historical isolation among different disciplines, institutes, and funding schemes (Soininen et al. 2015). In reality, however, ecosystems are not isolated, and numerous studies and documented examples highlight the importance of cross-ecosystem interactions and connectivity within and across ecosystems (Marczak et al. 2007; Marcarelli et al. 2011; Bartels et al. 2012; Subalusky and Post 2019). For instance, adjacent food webs may be linked by cross-boundary subsidies, as observed in the reciprocal flows of invertebrate prey between streams and their adjacent riparian zones (Nakano and Murakami 2001; Baxter et al. 2005). Terrestrial invertebrates can provide subsidies to freshwater organisms such as fish by falling into streams, whereas the emergence of adult aquatic insects can provide subsidies to riparian consumers such as spiders, birds, and bats, establishing a reciprocal flux between the two ecosystems. Marine and terrestrial ecosystems are also deeply connected, especially on islands. Seabirds forage in the ocean but nest on land, transferring nutrients across ecosystem boundaries through the production of large quantities of guano, which can enhance the productivity of many terrestrial ecosystems (Wilder et al. 2022) and their surrounding coastal ecosystems, such as coral reefs (Savage 2019; Benkwitt et al. 2022).

Most research on resource subsidies has focused on native species, particularly on a few conspicuous taxa known to mediate strong cross-ecosystem flows, such as salmon during their spawning runs, storm-driven seaweed, and arthropod emergence (Sato et al. 2021). Although numerous studies have examined non-native species and their ecological impacts (Andersen et al. 2004; Crowl et al. 2008; Pyšek et al. 2008; Mollot et al. 2017), far less attention has been given to their role as mediators of such flows. However, many non-native species can dramatically reshape community and ecosystem processes by introducing new subsidies or reducing existing ones. Although some studies have attempted to address this topic (Croll et al. 2005; Novais et al. 2015), subsidy effects are often indirect, taxonomically biased, or not the original focus of ecological studies, making them challenging to investigate. This has created a gap in the understanding of the effects of non-native species on resource subsidies, potentially leading to an underestimation of the breadth of their ecological impacts.

Recently, a study by Peller and Altermatt (2024) compiled emerging examples demonstrating the cross-ecosystem impacts of non-native species worldwide. However, that study also highlighted the need for a review collating the available information to provide a more comprehensive overview of existing knowledge and research gaps pertaining to the effects of non-native species on resource subsidies. For this purpose, a review of studies examining resource subsidies affected

by non-native species was conducted to (1) characterize the temporal trends, geographic areas, and methodological approaches used in studies of resource subsidies mediated by non-native species; (2) synthesize how non-native species alter the magnitude, direction, and dynamics (e.g., timing and duration) of resource subsidies across ecosystems and their implications for ecosystem functioning; and (3) identify key knowledge gaps and priority directions for future research. By systematically synthesizing this information, this review provides the first comprehensive overview of invasion-affected resource subsidies, offering a foundation for future research and the management of ecosystems and their connectivity.

Methods

A systematic approach was chosen because it ensures transparency and reproducibility while providing a comprehensive synthesis across taxa and ecosystems.

The literature search was conducted using Scopus. The search was confined to the subject areas of "Agricultural and Biological Sciences" and "Environmental Science." The following search terms were used: (trophic OR spatial OR resource* AND subsid*) AND (exotic OR alien OR invasive OR introduced OR pest OR non-native OR non-indigenous). These terms were searched within article titles, abstracts, and keywords. The document type was restricted to articles, the source type to journals, and the language to English. The search encompassed all articles published up to the completion of the literature search on 31 December 2024 and yielded 307 articles, which were then evaluated for relevance to the proposed theme. Articles that did not fully correspond to the topic of resource subsidies mediated by non-native species were excluded from further analysis (n = 242). In addition to the articles obtained from the Scopus search, the references within these articles were also reviewed to identify additional relevant studies, thus complementing the list for analysis (n = 78). Therefore, 143 papers met the criteria and were selected for this review. For each study, the following information was recorded: (1) the continent (Africa, Asia, Europe, North America, Oceania, and South America) where the research was conducted; (2) the publication year; (3) the types of donor and recipient ecosystems, categorized as terrestrial, freshwater, and marine; (4) the taxonomic group of the non-native species mediating the subsidy; (5) the taxonomic group of the affected native biota; (6) the methodologies used; and (7) the biotic and abiotic variables reported.

Taxonomic information was standardized and aggregated into the following groups: Plantae, Algae, Actinopterygii, Mammalia, Aves, Arthropoda, Bivalvia, Amphibia, and Reptilia. Unidentified or mixed taxa (e.g., Fungi, Bacteria, Microbes, and Invertebrates) were recorded as "Others." Methodological categories were classified as controlled experiments, diet content analysis, DNA analysis, elemental analysis, field-based studies (field observations, field sampling, and experiments), modeling, remote sensing, stable isotope analysis, and field-monitoring techniques (tagging, telemetry, and camera trapping). When multiple methodological categories were applied within the same study, each was recorded separately. Biotic variables included measures such as abundance, biomass, diversity, decomposition, and reproduction. Additional biotic parameters categorized as other included fitness, survival, feeding rates, and behavioral traits. Abiotic variables encompassed carbon and nitrogen concentrations, organic matter, pH, oxygen, conductivity, and temperature. Additional abiotic parameters categorized as other included light availability, nutrient concentrations, and hydrological characteristics. All percentages and

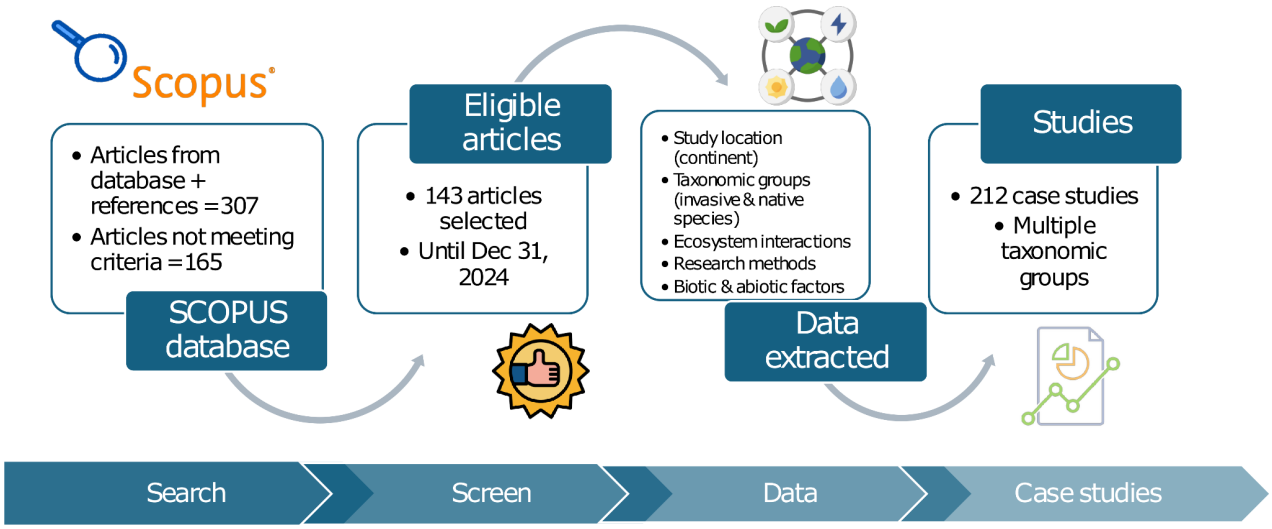

Figure 1. Flowchart showing the review process, including the literature search, data screening, data collection, and final case studies.

frequencies presented in the Results were calculated based on the total number of case studies (n = 212), except for the spatial distribution of the studies, for which the total number of papers was used (n = 143) (Fig. 1).

The collected data (see Suppl. material 1) were processed using RStudio (R version 4.4.0; R Core Team 2025). To visually highlight the links between non-native and native species and the cross-ecosystem interactions, a flowchart was created using the R package networkD3 (Allaire et al. 2017). The packages rnaturalearth (South and South 2017) and rnaturalearthdata (South et al. 2017) were used to construct a map indicating the number of studies per continent.

General patterns

Temporal distribution

Although the number of publications on the effects of non-native species on resource subsidies identified by the literature search initially increased over time, it appears to have stagnated over the past decade. The number of papers increased rapidly from 2000–2004 to 2005–2009, peaking in 2010–2014 (Fig. 2). These trends paralleled the acceleration in the number of published articles over time (Fire and Guestrin 2019; WordsRated 2023) and aligned with the increasing prominence of topics such as biological invasions and ecosystem connectivity in ecology and conservation science (Polis et al. 1997; Post 2002; Pyšek et al. 2020). However, publication output declined between 2015 and 2019, followed by a slight resurgence during 2020–2024, despite the potential disruptions associated with the COVID-19 pandemic (Sloane and Zimmerman 2021).

Spatial distribution

North America dominated research on resource subsidies mediated by non-native species (Fig. 3). Europe ranked second in the number of articles produced, but only a few countries (i.e., the UK, Germany, France, Spain, and Portugal) were represented. Similarly, most South American countries were not represented, with research conducted only in Patagonia and Tierra del Fuego (Argentina and Chile). Oceania, however, presents a paradox: despite hosting some of the world's most

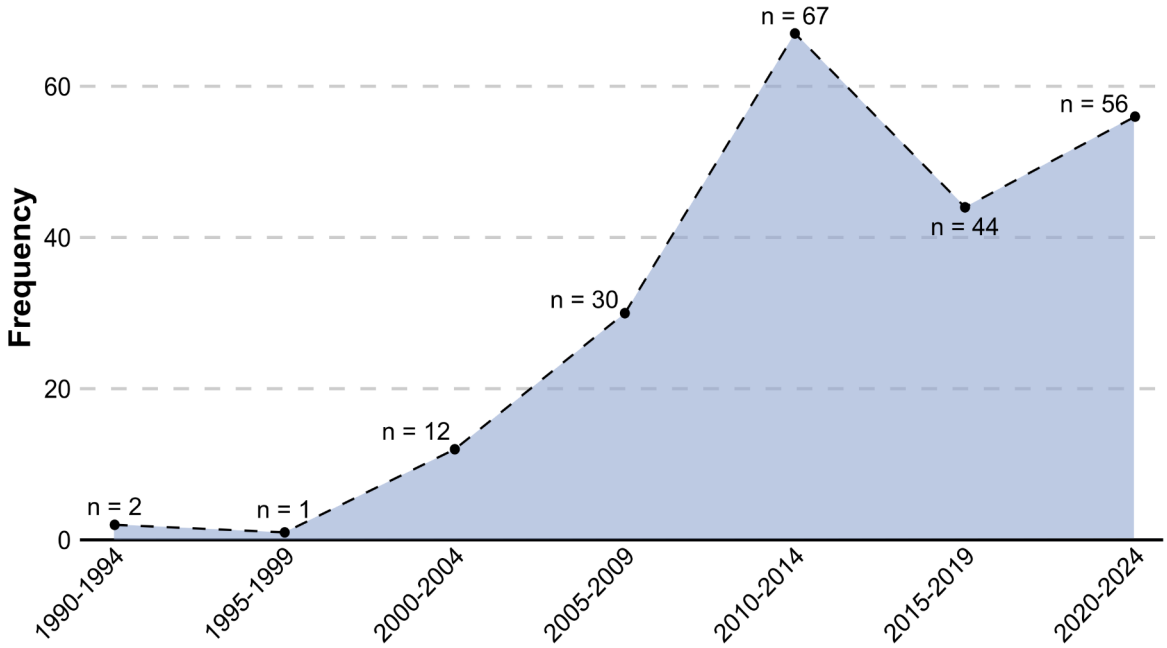

Figure 2. Number of publications produced on the topic of resource subsidies mediated by non-native species.

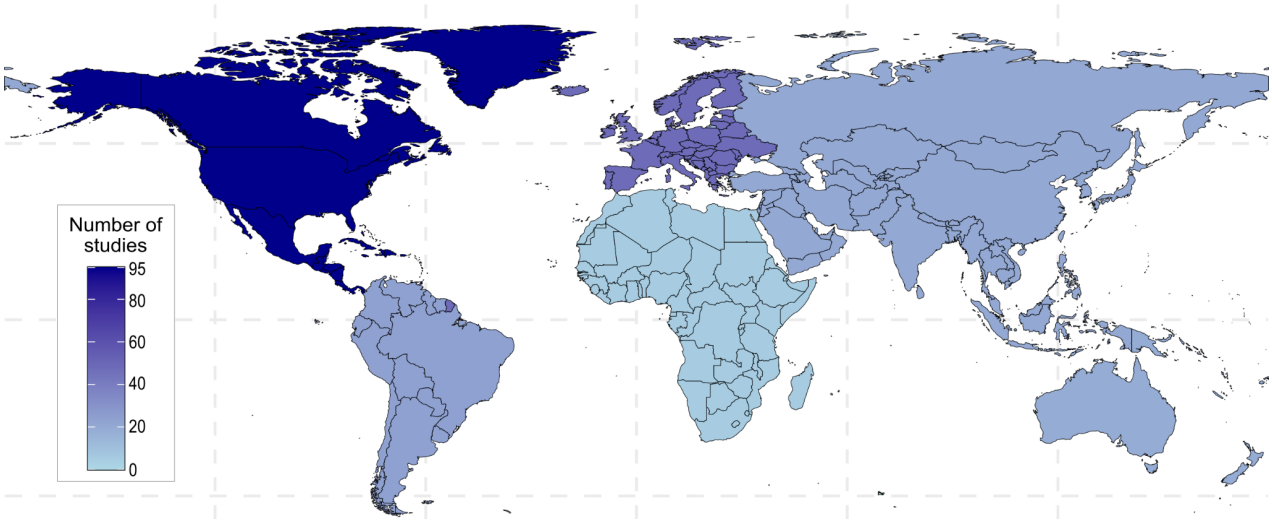

Figure 3. Number of publications per continent on the topic of resource subsidies mediated by non-native species.

threatened endemic biodiversity and facing severe impacts from non-native species (Invasive Species Council 2022), few studies have examined connectivity between ecosystems mediated by biological invasions, as only 12 studies were identified. Similarly, only a relatively small number of studies were identified in Asia (n = 11), with the majority originating from islands that are geographically located in Asia but politically aligned with countries on other continents, mainly the United Kingdom. Finally, only four studies published in Africa were identified.

Despite the greater biodiversity present in the tropics, the vast majority of research on biological invasions has been conducted in temperate regions (North America, Europe, and Australia), with minimal contributions from the tropics, except for some island systems (Hulme et al. 2013; Chong et al. 2021). This pattern is supported by the data and also corresponds to the hotspots of non-native species richness in countries such as the USA (Turbelin et al. 2017) and the greater investment in re-

search in high-income economies such as the USA, Germany, and the United Kingdom (UK). Despite the ecological significance of tropical ecosystems, these regions are largely underrepresented in the review yet are increasingly subject to biological invasions (Zenni et al. 2022). Given the limited number of studies conducted in tropical regions, there is a pressing need for further research that could provide important information and reveal broader patterns on the topic.

Methodological categories used

Field-based studies were the most commonly used technique (43%) (Fig. 4). Examples include studies on introduced predators and the effects of temperature on aquatic insect emergence in alpine lakes and on carrion subsidies from mass mortalities of the Asian clam *Corbicula fluminea* affecting terrestrial and aquatic communities (Novais et al. 2015; Novais et al. 2017; Owens et al. 2023).

Stable isotope analysis was the second most widely used technique in the reviewed studies (17%). It has become an invaluable tool for reconstructing diets and food webs, characterizing trophic relationships, elucidating patterns of resource allocation, and estimating the proportion of elemental fluxes across different trophic levels and ecosystems (Majdi et al. 2018). Consequently, the number of studies using this method in trophic ecology has increased over the past decades (Boecklen et al. 2011). Diet content analysis is another method widely used in trophic ecology (Winemiller 1990; Majdi et al. 2018) and was frequently used in studies examining the impacts of non-native species on native species across various ecosystems, given its accessibility and applicability at relatively large spatial and temporal scales.

Controlled experiments were employed in several studies (10%). This approach enable the controlled manipulation of key environmental variables while retaining ecological realism, addressing the complex interplay among environmental conditions, human disturbance, and the establishment of non-native (Jackson et al. 2013). For example, one study examined how natural and artificial resource subsidies influenced the reproduction and establishment of the introduced topmouth gudgeon (*Pseudorasbora parva*) using replicated pond mesocosms (Jackson et al. 2013). Elemental analysis was similarly frequent (8.5%), especially in case studies investigating

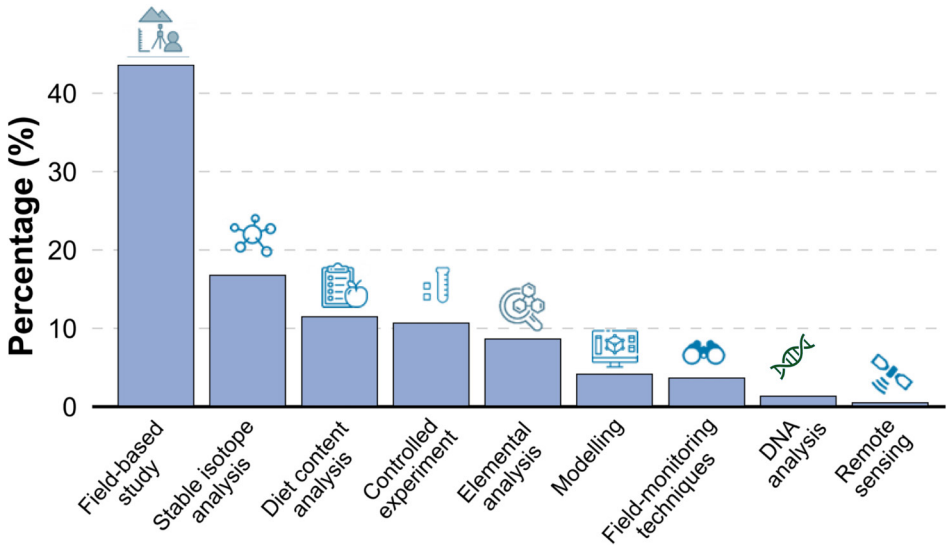

Figure 4. Percentage of methodological categories used in the 212 case studies analyzed.

the quality of subsidies provided by non-native plants and their transport to freshwater ecosystems (Kennedy and Hobbie 2004; Lecerf et al. 2007; Maerz et al. 2010).

Less commonly used methods included DNA analysis (1.2%), remote sensing (0.4%), and field-monitoring techniques (3.6%). Although each of these accounted for only a small percentage of studies, they can offer valuable complementary insights into species movement, behavior, and spatial patterns, all of which are crucial for understanding the broader implications of non-native species and their associated subsidies. Field observation, in particular, was used to document incidental observations. For example, while conducting unrelated research, scientists observed an adult male red fox catching a common carp (*Cyprinus carpio*) along the shore, providing valuable insight into a novel mechanism of resource subsidy transfer (Tobajas and Díaz-Ruiz 2022).

Biotic and abiotic factors measured

Many studies measured impacts on native species using various biotic parameters (n = 196) (Fig. 5a). The most commonly assessed factor in impacted communities and species was biomass (26%), reflecting the focus on how non-native species alter energy flow or structural biomass within invaded ecosystems. This was followed by abundance/density (19.3%) and decomposition (7.7%), suggesting a strong interest in how non-native species affect population sizes and ecosystem functions. Variables such as diversity (6.1%), productivity (5.1%), and growth (4.1%) were also reported, but less frequently. Finally, other biotic variables were reported in 42 studies (21.4%).

Several studies (n = 85) also investigated abiotic factors that could influence the flow of subsidies between ecosystems and the effects of non-native species (Fig. 5b). The most frequently measured abiotic variable was nutrient transfer (56.5%), especially carbon and nitrogen, which were directly associated with the

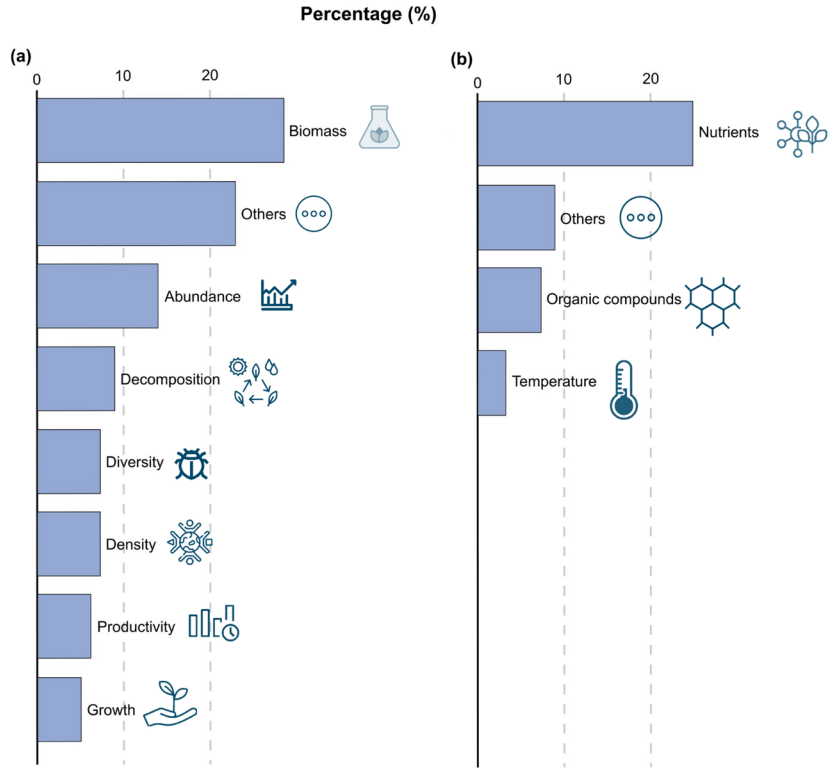

Figure 5. Percentage of the different (**a**) biotic and (**b**) abiotic factors assessed in the 212 case studies analyzed.

impacts of non-native species on cross-ecosystem subsidies. Organic compounds were assessed in 14 studies (16.5%), often in relation to allelochemicals produced by non-native plant litter and their effects on recipient communities, particularly in freshwater systems. Other abiotic variables were reported in 17 studies (20.0%). In contrast, temperature was the least commonly measured abiotic factor (7.1%) and was typically considered an indirect driver, influencing the magnitude or pathways of the impacts of non-native species on resource subsidies rather than being directly altered by the species.

Taxonomic distribution of non-native and native species

The majority of the publications reviewed here focused on certain non-native species distributed across a limited number of taxonomic groups (Fig. 6), typically those known to exert strong ecological or economic impacts (Thomsen et al. 2014). The taxonomic groups with the greatest number of studied resource subsidies were Plantae (angiosperms and gymnosperms; n = 61), Actinopterygii (fish; n = 54), and Mammalia (mammals; n = 46).

Riparian plants such as *Lythrum salicaria* and *Prunus padus* received considerable attention for their role in altering litter quality and nutrient inputs across terrestrial–freshwater boundaries (Mineau et al. 2012; Riedl et al. 2019). Salmonid species dominated many studies in aquatic ecosystems because of their dual

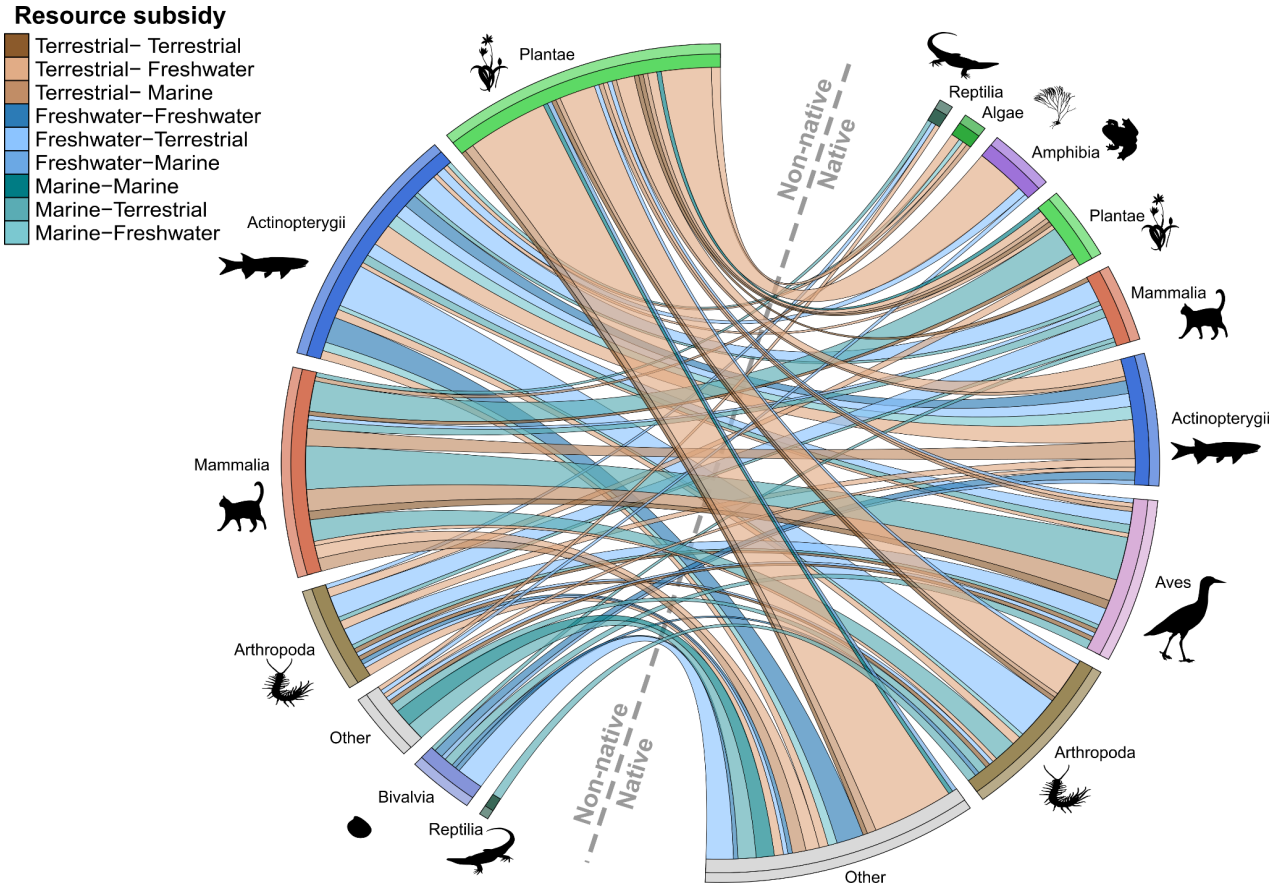

Figure 6. Sankey diagram showing the relationship between non-native taxonomic groups (left) and affected native taxa (right) through the direct and indirect effects of non-native taxa on resource subsidies across different ecosystem linkages. Line thickness is proportional to the number of reported cases, illustrating major research foci and taxonomic–geographic biases in subsidy mediation.

status as ecosystem engineers and economically valuable fish in aquaculture and recreational fisheries (Vigliano et al. 2007; Dettmers et al. 2012). Many studies conducted in South America mirrored earlier research from the native range of salmonids, illustrating how established research frameworks and funding priorities can shape the global taxonomic distribution of biological invasion studies. In many studies (n = 37), mammals were identified as the group of non-native species threatening the greatest number of species, particularly rodents (*Rattus* spp.) and feral cats (*Felis catus*), which primarily prey on birds (Dueñas et al. 2021). They are disproportionately represented because of their well-documented roles in seabird colony collapse and nutrient reductions on islands (Wardle et al. 2009; Benkwitt et al. 2020; Linhares and Bugoni 2023). Similarly, beavers (*Castor canadensis*) introduced to Tierra del Fuego have received attention because of their known ecosystem-engineering effects on terrestrial–freshwater connectivity (Henn et al. 2016). Other taxonomic groups, such as Arthropoda (mainly malacostracans [n = 14], with some cases focusing on insects [n = 6]) and Bivalvia (bivalves; n = 14), were central to several case studies. In contrast, the category "Others" included less-studied groups, such as Phaeophyceae (brown algae; n = 3). The flows identified here thus indicate that Actinopterygii and Mammalia primarily mediated aquatic–terrestrial linkages, whereas Plantae contributed mainly to terrestrial–freshwater or terrestrial–terrestrial exchanges. In contrast, Arthropoda and Bivalvia featured in studies of benthic and detrital pathways linking aquatic and terrestrial systems.

Patterns in cross-ecosystem subsidies mediated by non-native species revealed strong asymmetries across taxa, ecosystem linkages, and continents (Fig. 6). The majority of documented interactions involved terrestrial–freshwater (33%) and freshwater–terrestrial (23%) linkages, whereas purely aquatic (e.g., freshwater–freshwater and marine–marine) or within-realm terrestrial exchanges were comparatively rare. Among taxonomic groups, Arthropoda (n = 36, 18%), Actinopterygii (n = 29, 15%), and Mammalia (n = 17, 9%) dominated the recorded cases, together accounting for over half of all observations, whereas algae (n = 5, 2.5%) and Reptilia (n = 3, 1.5%) contributed only marginally. The direction of subsidy flows reflected the ecological traits of donor taxa—e.g., aquatic insects and fish transferring organic matter or nutrients to terrestrial consumers—highlighting the importance of bidirectional coupling between aquatic and terrestrial systems. Overall, the network structure indicates that current knowledge of non-native subsidies is heavily biased toward animal-mediated exchanges in temperate regions and that interactions involving tropical systems and microbial or primary-producer pathways remain poorly documented.

Cross-ecosystem interactions

Cross-ecosystem linkages mediated by non-native species were dominated by terrestrial–freshwater (n = 70) and freshwater–terrestrial (n = 46) interactions, together accounting for more than half of all documented cases. The dominance of terrestrial–freshwater pathways reflect the prevalence of research on riparian ecosystems, where bidirectional flows of nutrients, prey, and detritus are well documented. Exchanges involving marine–terrestrial or terrestrial–marine connections were less frequent (n = 41 and n = 19, respectively), whereas purely aquatic linkages, such as freshwater–freshwater and marine–marine interactions, were comparatively rare.

General patterns

Terrestrial–freshwater interactions emphasize the critical link between streams and riparian zones, which are widely recognized as interdependent systems connected mainly by reciprocal flows of invertebrate prey (Larsen et al. 2016). The reviewed publications predominantly examined terrestrial–freshwater interactions, which were studied across all continents. These studies are highly relevant, given the high biodiversity per unit surface area in freshwater ecosystems and their significant transformation by non-native species from various taxonomic groups (Strayer 2010; Simberloff et al. 2013; Havel et al. 2015). Reported interactions were largely mediated by non-native riparian plants, which provide subsidies through litter production. Another important taxonomic group was Actinopterygii, for which the primary mechanism was predation on terrestrial prey subsidies falling into streams, thus reducing their availability to native species (Rolla et al. 2018; Kreutzweiser et al. 2019; Table 1).

Freshwater–terrestrial interactions were another well-studied category, with non-native fish playing a central role. The main subsidy involved was the emergence of aquatic insects, with non-native fish preying on insects during their aquatic larval stage, thereby interrupting their emergence as adults into terrestrial ecosystems. This situation affects riparian consumers and terrestrial food webs because the emergence of adult insects from streams constitutes a substantial export of benthic production to riparian consumers such as birds, bats, lizards, and spiders (Baxter et al. 2005; Epanchin et al. 2010; Jackson et al. 2016).

Marine–terrestrial interactions were observed on almost all continents except Africa. Most of the linkages from Oceania originated from marine–terrestrial case studies. The primary taxonomic group responsible for these interactions was Mammalia, particularly non-native rats, which reduce nutrient and guano flows from marine to terrestrial ecosystems by preying on seabirds (Pascoe et al. 2022).

Some studies also focused on terrestrial–marine interactions, which were mainly examined on North American and Asian islands. The primary processes driving these interactions were predation by non-native rats on seabirds, which reduced nutrient flow to coastal ecosystems, and the invasion of monocotyledonous plants, which reduced native tree abundance and, consequently, seabird abundance. This decrease in seabird abundance resulted in reduced nutrient transport to coastal ecosystems, thereby decreasing productivity (McCauley et al. 2012; Graham et al. 2018; Gunn et al. 2023).

Marine–freshwater case studies were primarily conducted in South America and were largely mediated by introduced salmonids such as Atlantic salmon, *Salmo salar*, and coho salmon, *Oncorhynchus kisutch*, which migrate from marine to freshwater ecosystems, providing nutrient subsidies to freshwater communities (Dunlop et al. 2021; Muñoz et al. 2021).

In the opposite direction (i.e., freshwater–marine), only one example was retrieved, concerning the die-off of the non-native Asian clam (*Corbicula fluminea*), whose soft tissues were consumed by European seabass (*Dicentrarchus labrax*) in an Iberian estuary (Ilarri et al. 2011). Although unpublished—or at least not retrieved in the review—other examples may exist and may encompass, for example, the transport of water hyacinth (*Pontederia crassipes*) or Brazilian waterweed (*Egeria densa*) from rivers to coastal areas during floods (Ronaldo Sousa, personal observation). The massive biomass transported may have consequences for marine biodiversity and ecosystem functioning, with potential impacts on scavengers and nutrient cycling.

Table 1. Spatial subsidies mediated by non-native species among different ecosystems (marine, freshwater, and terrestrial).

Species	Donor Ecosystem	Recipient Ecosystem	Description	Subsidy	References
Lymantria dispar	Terrestrial	Terrestrial	The non-native gypsy moth undergoes periodic outbreaks and represents a superabundant food resource for predators, particularly native cuckoos (*Coccyzus erythropthalmus* and *C. americanus*).	Addition	Barber et al. 2008
Melaleuca quinquenervia			In the presence of this non-native plant, panthers need to move farther to access the resources they need, creating a unique spatial-flow connection between ecosystems that did not exist in the uninvaded state.	Addition	Julian et al. 2012
Salvelinus fontinalis		Freshwater	Non-native brook trout consume many terrestrial invertebrate subsidies, reducing this resource for other species.	Reduction	Rolla et al. 2018
Lythrum salicaria			A high floral density of non-native purple loosestrife increases adult dragonfly oviposition and subsequently increases larval dragonfly abundance in aquatic ecosystems.	Addition	Burkle et al. 2012
Rattus rattus		Marine	By depleting seabird populations, non-native rats reduce the natural flow of nutrient subsidies (guano) to coral reefs, thereby reducing the biomass of coral reef fish.	Reduction	Benkwitt et al. 2020
Cocos nucifera			Reductions in native tree abundance reduce seabird abundance, diminishing the movement of nutrients to the marine environment, reducing zooplankton abundance, and ultimately eliminating manta ray (*Manta birostris*) use of native forest coastlines.	Reduction	McCauley et al. 2012
Dreissena polymorpha and *D. rostiformis bugensis*	Freshwater	Freshwater	Grazing by non-native mussels dramatically alters the pelagic energy channel by reducing the offshore transport of nutrients and energy. As mussels reduce the availability of pelagic energy, fish and invertebrates compensate by deriving more energy from alternative nearshore benthic or detrital energy channels.	Reduction	Turschak et al. 2014
Oncorhynchus spp.			In some introduced ranges, salmon forage in lakes and migrate to streams to spawn, connecting different freshwater ecosystems.	Addition	Janetski et al. 2014
Oncorhynchus mykiss and *Salmo trutta*		Terrestrial	Invaded sites have decreased prey availability for riparian spiders that rely heavily on insect emergence.	Reduction	Jackson et al. 2016
Pomacea maculata			High densities of *P. maculata* populations could facilitate snail kites by providing supplemental food resources.	Addition	Cattau et al. 2016
Pontederia crassipes		Marine	During floods, massive quantities of water hyacinth biomass are transported from rivers to marine areas.	Addition	Ronaldo Sousa personal observation
Corbicula fluminea			During die-offs of *Corbicula fluminea*, their soft tissues are consumed by European seabass (*Dicentrarchus labrax*).	Addition	Ilarri et al. 2011
Caulerpa taxifolia	Marine	Marine	Detritus from non-native algae subsidizes invertebrate communities on intertidal mudflats.	Modification	Bishop and Kelaher 2013
Codium fragile			Productive macroalgae can subsidize dense detritivore populations in the supralittoral, littoral, intertidal, and deep benthic zones.	Modification	Krumhansl and Scheibling 2012
Alopex lagopus		Terrestrial	Arctic fox predation on seabirds reduces nutrient subsidies from marine ecosystems. The resulting impoverished soils affect the plant community.	Reduction	Maron et al. 2006
Sargassum muticum			Productive macroalgae subsidize beaches and adjacent terrestrial areas.	Addition	Rossi et al. 2010
Silurus glanis		Freshwater	The non-native European catfish preys on sea lampreys during their migration from marine to freshwater ecosystems.	Reduction	Boulêtreau et al. 2020
Oncorhynchus tshawytscha			Anadromous non-native Pacific salmonids deposit large quantities of energy and nutrients of marine origin into rivers and lakes through reproductive products, excretion, and carcasses.	Addition	Arismendi and Soto 2012; Muñoz et al. 2021, 2022

Freshwater–freshwater interactions were studied primarily in North America and were mainly mediated by non-native salmonids that live in lakes and migrate to streams to spawn, transferring nutrients between freshwater ecosystems (Levi et al. 2013; Hermann et al. 2020).

Only a few studies examined marine–marine interactions, mainly focusing on the effects of detritus transported from non-native estuarine plants or algae on invertebrates (Taylor et al. 2010; Krumhansl and Scheibling 2012; Wang et al. 2022). Another example involves non-native bryozoans that may increase the amount of material eroded from subtidal kelp beds (*Saccharina longicruris* and *Laminaria digitata*), thereby subsidizing communities inhabiting deeper offshore waters (Krumhansl et al. 2011).

Ten studies examined terrestrial–terrestrial interactions. Examples include non-native yellow crazy ants (*Anoplolepis gracilipes*) that benefit from carbohydrate subsidies provided by introduced honeydew-producing scale insects, enabling them to expand their foraging ranges and transport resources from canopy treetops to the forest floor (Bradford et al. 2012; Wittman et al. 2018). Additionally, the presence of the non-native plant *Melaleuca quinquenervia* altered the movement patterns of Florida panthers (*Puma concolor coryi*) by forcing them to move farther to access the resources they needed, creating novel spatial connections between ecosystems that were previously unlinked in the uninvaded area (Julian et al. 2012).

Addition of a novel subsidy

Non-native species can introduce a wide variety of novel resource subsidies, including nutrients, organic matter, carrion, prey, floral resources, and even pollutants, thereby reshaping the movement of energy and materials across ecosystem boundaries. Such subsidies span a wide spectrum of mechanisms and taxa. Introduced salmon (*Oncorhynchus* spp.) can transport marine-derived nutrients and contaminants into freshwater systems, enriching otherwise oligotrophic environments while simultaneously modifying food-web structure (Gerig et al. 2019; Muñoz et al. 2022; Brandt et al. 2024). Mass mortalities of bivalves such as *Corbicula fluminea* may generate carrion pulses that subsidize terrestrial and aquatic decomposer communities, influencing microbial activity and nutrient cycling (Sousa et al. 2012; Novais et al. 2015, 2017). Terrestrial plants, including *Lythrum salicaria* and *Lonicera maackii*, contribute large inputs of organic matter and floral resources to aquatic systems, with measurable effects on benthic communities and primary productivity (Burkle et al. 2012; Custer et al. 2017).

Introductions of novel prey, such as *Lepus europaeus*, create new trophic interactions among native predators through kleptoparasitism, altering competitive hierarchies (Perrig et al. 2023). Likewise, alternative prey subsidies—such as raccoons exploiting non-native intertidal clams—can increase predator populations and intensify pressure on native fauna (Simmons et al. 2014). Across these cases, the addition of new energy and material pathways not only modifies local food-web dynamics but also strengthens or creates previously absent ecosystem linkages, demonstrating the potential for non-native species to restructure community composition and ecosystem functioning across spatial scales.

Reduction of an already existent subsidy

Non-native species can also reduce existing resource subsidies, weakening cross-ecosystem connectivity through a variety of mechanisms. On tropical islands, *Rattus* spp. prey on seabird chicks and eggs, collapsing colonies and halting the transfer of marine-derived nutrients to terrestrial soils and back to coastal ecosystems (McCauley et al. 2012; Linhares and Bugoni 2023). In riparian systems, the green alder sawfly (*Monsoma pulveratum*) and European bird cherry (*Prunus padus*) reduce the supply of terrestrial invertebrate prey to streams, either through the defoliation of native vegetation or replacement by less productive non-native plants (Roon et al. 2016; Roon et al. 2018). Direct predation by non-native fish and the amphipod *Dikerogammarus villosus* further suppresses the emergence or availability of aquatic insects, diminishing food resources for riparian predators such as spiders (Gergs et al. 2014; Jackson et al. 2016; Rolla et al. 2018). Behavioral responses can also interrupt material flows, as demonstrated by freshwater crocodiles (*Crocodylus johnstoni*) avoiding terrestrial foraging after being poisoned by invasive cane toads (*Rhinella marina*), effectively severing aquatic–terrestrial energy transfer (Aiyer et al. 2022).

Modification of subsidy

Another mechanism by which non-native species can alter linkages between ecosystems is through the modification of spatial subsidies. Instead of merely adding novel subsidies or interrupting subsidy flows, non-native species can modify existing subsidy pathways. For example, the non-native river red gum (*Eucalyptus camaldulensis*) sheds significantly more leachate and exhibits less microbial and detritivore breakdown than the native leadwood (*Combretum imberbe*) (Wasserman et al. 2021). The breakdown rates and macroinvertebrate colonization of leaf litter from various native and non-native plants also vary according to resource quality and palatability to consumers. This variation is often more dependent on resource quality and nutrient imbalances in leaf litter than on the origin of the plants (Hladyz et al. 2009). In fact, the dominance of some non-native plants can affect aquatic detrital-pool dynamics and lead to a plant community predominantly composed of more recalcitrant species, which generally have a higher leaf C:N ratio. This situation may negatively affect amphibian populations because differences in the quality of detritus produced by non-native species compared with native species can affect tadpole performance, reducing subsidies to terrestrial consumers and disrupting cross-ecosystem connectivity (Maerz et al. 2010).

Similarly, the non-native bivalve *C. fluminea* can alter nutrient cycling in the benthic environment of freshwater ecosystems. This species releases more nitrogen through its biodeposits than the native bivalve *Elliptio crassidens*. Consequently, *C. fluminea* has the potential to profoundly affect organic matter dynamics and nutrient cycling in streams, affecting the linkage between the water column and benthic ecosystems (Atkinson et al. 2010). Likewise, non-native armored catfish (Loricariidae: *Pterygoplichthys*) can modify nutrient dynamics in freshwater ecosystems by creating biogeochemical hotspots. Through their diel movements and dense daytime aggregations, these fish increase local concentrations of dissolved nutrients through excretion in nutrient-limited streams. This may alter nutrient cycling and availability for other organisms, effectively modifying the quality and flow of resource subsidies within and across ecosystem boundaries (Capps and Flecker 2013).

Another example involves variation in the form of marine detritus, or wrack, washing up in coastal terrestrial ecosystems. Different types of wrack deposits may not be uniformly used by invertebrates because their nutritional value can differ between the non-native and native species providing the wrack. Evidence suggests that the nutritional content and microclimatic conditions of wrack deposits can affect macrofaunal assemblages (Rodil et al. 2008). Therefore, marine subsidies might be altered depending on the species present, changing the composition of the communities receiving these subsidies.

Biological invasions in connected ecosystems: the role of resource subsidies

As demonstrated above, non-native species can play a critical role in affecting resource subsidies across ecosystems. However, the impacts of these subsidies depend on four key factors: quantity, quality, timing, and duration (following Subalusky and Post 2019). Understanding these factors is vital for predicting and managing the ecological outcomes of biological invasions in both natural and human-altered environments. Recognizing the limitations arising from the lack of knowledge about resource subsidies mediated by non-native species—which can either bolster or destabilize ecological processes depending on the specific context—underscores the need for a broader, integrative framework that explicitly considers cross-ecosystem processes and feedbacks at larger spatial and temporal scales.

Quantity of resource subsidies

The amount of a resource subsidy that enters an ecosystem is one of the most straightforward but critical variables determining its effects, and non-native species can clearly affect the quantity of prey, detritus, energy, or nutrients entering an ecosystem.

In systems where nutrient availability is naturally limited, a sudden increase in resource inputs from non-native species can stimulate primary productivity, leading to greater biomass and increased consumer populations. In nutrient-poor streams, the influx of leaf litter from surrounding forests provides the carbon necessary to support decomposers and primary consumers, which in turn fuel higher trophic levels. For instance, *Falcataria moluccana* (albizia) is a nitrogen (N)-fixing tree that increases nitrogen availability in invaded ecosystems, serving as a significant N source for benthic primary producers and potentially driving bottom-up changes in the food web. By displacing particulate organic matter and macroalgae as the primary food sources for lower-level consumers, albizia also indirectly provides carbon (C) and N to higher-level consumers (Atwood et al. 2010). Taylor et al. (2010) found that the quantity of detritus from the non-native *Caulerpa taxifolia* had a stronger impact and that variations in C:N ratios between oligotrophic and eutrophic environments influenced the effects of high detrital loads. However, an excessive quantity of subsidies can lead to ecosystem degradation. In freshwater ecosystems, for example, nutrient overloading can result in eutrophication, whereby excessive algal growth depletes oxygen in the water, which may be detrimental to most aquatic life. This situation has been described in response to mass mortalities of non-native bivalves (Ilarri et al. 2011; Bódis et al. 2014; Novais et al. 2015). The relationship between the quantity of a subsidy and its ecological effects is often nonlinear, with low levels providing beneficial inputs but high levels

leading to negative consequences (Odum et al. 1979). Ecosystems have thresholds for resource inputs, and crossing these limits can cause abrupt changes, leading to declines in biodiversity and changes in ecosystem functioning. However, these thresholds have not been assessed in invaded ecosystems.

Quality of resource subsidies

The quality of resource subsidies refers to the specific composition or type of materials entering an ecosystem. Not all subsidies are equally beneficial or harmful—some are more easily assimilated by the receiving ecosystem, whereas others may be difficult to process or may be toxic. For example, studies have shown that toxic compounds from non-native plants can leach into freshwater ecosystems, affecting various organisms, such as *Daphnia* and developing anuran larvae (Griffiths et al. 2021; Diller et al. 2022, 2023; Iglesias-Carrasco et al. 2022).

High-quality resource subsidies tend to be those that closely match the nutrient requirements or biological characteristics of the recipient ecosystem. For instance, in terrestrial ecosystems, nitrogen deposition from natural sources such as decomposing leaf litter can stimulate plant growth in nitrogen-limited soils, enhancing productivity and biomass. Kuglerová et al. (2017) demonstrated that some non-native plants can have faster decomposition rates than native species. Their experiment showed that the non-native *Impatiens glandulifera*, with its high leaf nitrogen content, supported the highest densities and richness of macroinvertebrates. This suggests that consumer communities aggregate around the highest-quality litter, accelerating litter breakdown rates regardless of whether the source is native or non-native. Similarly, Stephens et al. (2013) found that three non-native plant species provided conditions for the development of amphibian metamorphs that were heavier, had shorter larval periods, and showed higher survival rates than those associated with native plants, suggesting that litter nitrogen may be a limiting resource influencing the export of metamorphic frog biomass from ephemeral ponds. Similarly, inputs of highly digestible prey into an ecosystem can increase predator populations by providing an easily accessible energy source. A notable example involves raccoons (*Procyon lotor*), which selectively forage on non-native intertidal clams of optimal size, maximizing their energetic returns. These more profitable non-native clams effectively subsidize raccoon populations, demonstrating how non-native prey can influence predator dynamics (Simmons et al. 2014).

In contrast, low-quality subsidies may not be readily used by the recipient ecosystem, although they may still disrupt ecological balance. For example, lignin-rich organic matter from certain non-native plant species, such as water hyacinth transported from rivers into marine ecosystems during floods (Ronaldo Sousa, personal observation), may be difficult to decompose and may alter decomposition rates and nutrient-cycling processes. The impact of subsidy quality is also linked to the adaptability of organisms in the recipient ecosystem. Some species can capitalize on low-quality or novel resources, whereas others may be disadvantaged, leading to shifts in species composition and ecosystem functioning. The invasion process may be highly amenable to assessments of this situation, but no study addressing this topic is known.

Resource subsidies, such as salmon spawning migrations, can transport marine-derived materials that enhance inland productivity while simultaneously increasing contaminant exposure across aquatic–terrestrial boundaries (Brandt et al. 2024; Twining et al. 2025). When these migrations involve non-native salmonid

populations introduced outside their native ranges, as in several regions of South America, they may act as invasion-mediated contaminant transfers. This remains largely unexplored and warrants further investigation because of its potential impacts on native biodiversity and ecosystem functioning (Brandt et al. 2024).

Timing of resource subsidies

The timing of resource subsidies can have profound effects on how they are integrated into ecosystems and on the resulting ecological outcomes. Natural ecosystems are often finely tuned to seasonal cycles of resource availability. When the timing of subsidies is altered, it can disrupt these cycles and lead to mismatches between resource availability and the needs of organisms (Shipley et al. 2022). For example, in response to climate change, some non-native species may change their phenology or migration timing, desynchronizing their availability to potential consumers, an issue that requires further research.

In many systems, resource subsidies arrive in predictable seasonal pulses that synchronize with the life cycles of organisms. The migration of salmon from the ocean to rivers provides a substantial influx of marine-derived nutrients to riparian ecosystems during the spawning season, which is then used by terrestrial and aquatic organisms. Chinook salmon (*Oncorhynchus tshawytscha*) have established non-native populations across Patagonia, providing salmon-derived nutrients to stream and forest food webs when they spawn and die. These nutrient pulses benefit a wide range of organisms, including invertebrates, birds, and mammals (Muñoz et al. 2022).

Duration of resource subsidies

The duration or persistence of resource subsidies determines whether their effects are temporary or long-lasting within an ecosystem. Some subsidies are short-term, arriving as a pulse and being quickly integrated, whereas others are more chronic, continuously influencing ecosystem dynamics over extended periods. Few studies have addressed this subsidy characteristic. For example, Novais et al. (2015, 2016) assessed the potential effects of non-native clams on terrestrial ecosystems over time, identifying clear temporal changes in some nutrients and in microbial and macroinvertebrate communities. However, the legacy effects may persist for more than 3 months, the duration of the study, and terrestrial plants, for example, may respond to this resource subsidy over a much longer period.

Pulse subsidies, such as a seasonal influx of nutrients or a temporary increase in prey availability, can lead to brief periods of heightened productivity. These pulses are often crucial for sustaining populations during otherwise resource-scarce periods. A clear example is introduced Pacific salmon (*Oncorhynchus* spp.), which provide pulsed resource subsidies to Great Lakes streams. During salmon runs, both native brook trout (*Salvelinus fontinalis*) and non-native brown trout (*Salmo trutta*) significantly increased their consumption rates. This resource pulse, particularly through the consumption of highly energetic and profitable salmon eggs, influenced trout foraging behavior and growth patterns (Hermann et al. 2020).

However, prolonged or chronic subsidies can lead to more permanent changes in ecosystem structure and function. In marine environments, the continuous input of organic matter can lead to hypoxia (low oxygen levels) and dead zones that persist over long periods, fundamentally altering ecosystem dynamics and making

recovery difficult. Bishop and Kelaher (2013) demonstrated that detritus from the non-native *Caulerpa taxifolia* influenced invertebrate communities on estuarine mudflats, which depend on litter subsidies from adjacent submerged aquatic vegetation. At low detrital inputs, *C. taxifolia* sustained more invertebrates and supported greater taxonomic diversity than native vegetation, but at high detrital loads, macroinvertebrate diversity declined, likely because of sediment hypoxia induced by excessive organic matter (Bishop and Kelaher 2013).

The persistence of subsidies also affects the resilience of ecosystems to disturbances. In cases where subsidies are predictable and cyclic, ecosystems may evolve adaptations that allow them to recover from disturbances. However, when the duration of subsidies is prolonged or unpredictable, ecosystems may lose their ability to recover, leading to long-term degradation.

The quantity, quality, timing, and duration of resource subsidies are crucial factors that shape ecosystem dynamics worldwide. Although subsidies can enhance productivity, support biodiversity, and maintain ecosystem functions, their effects are highly context-dependent because ecosystem characteristics may also play a significant role in the outcomes. Excessive or poorly timed subsidies can lead to ecosystem degradation, species loss, and trophic imbalances, particularly in systems that are not adapted to high levels of resource input. Global change drivers, such as biodiversity loss, land-use change, pollution, and climate change, are also expected to modify both the quality and quantity of subsidies (Larsen et al. 2016; Twining et al. 2025), potentially shifting their net effects on recipient ecosystems when coupled with biological invasions. By altering resource flows across boundaries, non-native species can extend their ecological footprint well beyond the systems in which they become established, with impacts cascading into connected ecosystems and expanding the range of stakeholders affected. Considering these complex interactions allows ecologists and policymakers to better predict ecological responses and develop management strategies that promote ecosystem resilience and sustainability in the face of biological invasions.

Caveats and future directions

Some aspects of the literature search methodology adopted in this review may have introduced bias into the results. In particular, the observed geographic imbalance may partly reflect language constraints, as the review included only English-language publications, likely excluding relevant studies published in Spanish, Portuguese, Russian, Chinese, and other languages (Angulo et al. 2021). This limitation suggests that the actual number of case studies on resource subsidies mediated by non-native species may be higher than reported here, especially in regions such as South America, Africa, and Asia, where locally conducted studies may be more frequently disseminated in national or regional languages. Additionally, this review relied on Scopus as the primary database for literature retrieval. Although Scopus is a comprehensive and widely used source, restricting the search to a single database may have led to the omission of relevant studies indexed elsewhere or accessible through alternative search strategies. This constraint could affect the completeness of the dataset and, consequently, the generality of the patterns identified, particularly if certain regions or taxa are unevenly represented in this database. Nevertheless, the use of backward reference screening partially mitigated this limitation by incorporating additional relevant studies beyond the initial search, and the overall patterns observed are

consistent with broader trends in the biological invasions literature. Although expanding the search to multiple databases and languages was beyond the scope of this study, future research could benefit from a more inclusive and multilingual approach to provide a more comprehensive and balanced understanding of this field.

In addition to these methodological limitations, the reviewed literature also reveals substantial gaps in taxonomic coverage, as many taxonomic groups remain overlooked. Invertebrates, despite their ubiquity and importance as bioindicators, are often grouped generically and rarely resolved to the class or order level. Nevertheless, arthropods—especially riparian spiders and aquatic insects—play critical roles in connecting freshwater and terrestrial food webs, and their responses to invasion-driven disruptions may have important ecological consequences (Jackson et al. 2016; Roon et al. 2018). Amphibians are also underrepresented, despite their dual life cycles across aquatic and terrestrial realms. No studies were found on how the chytrid fungus (*Batrachochytrium dendrobatidis*), a globally invasive pathogen, affects cross-ecosystem resource flows, although its severe effects on mortality likely disrupt both energy transfer and food-web stability (Capps et al. 2015; Zipkin et al. 2020; Fritz and Whiles 2021). Likewise, microbial groups such as fungi and bacteria, despite their fundamental roles in decomposition and nutrient cycling and their likely sensitivity to shifts in resource subsidies, were almost entirely absent from the reviewed literature, leaving a critical gap in understanding the functional consequences of invasions for biogeochemical linkages (but see Novais et al. 2017). This lack of case studies reflects an incomplete understanding of their ecological impacts and the mechanisms driving their invasions. Therefore, future research should explicitly address the roles of these taxonomic groups, particularly microorganisms such as fungi, bacteria, and viruses, in mediating resource subsidies (Marcarelli et al. 2011; Metcalf et al. 2016; Bahram and Netherway 2022; DeBruyn et al. 2025).

The study of trophic ecology is evolving rapidly. As technology improves, new tools and methodologies will be developed and applied to advance research and enhance the understanding of resource subsidies mediated by non-native species (Majdi et al. 2018; Ellis-Soto et al. 2021). Remote sensing, various types of sensors, and DNA analysis need to be explored further to fully understand the complexity of this topic. Advances in sensor technology and telemetry allow scientists to track movements and behaviors, even in small organisms, with great accuracy, enabling researchers to study the spatial dynamics of non-native species and their role in mediating resource subsidies (Ellis-Soto et al. 2021; Meira et al. 2024). Innovative approaches such as bioacoustics could also provide deeper insight into the ecological impacts of non-native species (see Meira et al. 2024). Studying changes in acoustic interactions within and between ecosystems may reveal shifts in species communication and behavior, potentially indicating broader shifts in ecosystem dynamics. Molecular techniques such as metabarcoding and environmental DNA (eDNA) analysis are also revolutionizing the detection and monitoring of non-native species across different ecosystems (Westfall et al. 2020). Future applications should move beyond detection toward quantifying trophic linkages and tracing resource flows. Combining molecular tools with biochemical tracers such as fatty acids and stable isotopes will enable finer-resolution analyses of energy pathways and clarify the mechanisms through which non-native species mediate cross-ecosystem exchanges (Liao et al. 2020; Ellis-Soto et al. 2021). Similarly, certain pollutants could be used as tracers to assess the role of non-native species in mediating resource subsidies (Brandt et al. 2024; Twining et al. 2025).

Beyond technological advances (for a review, see Meira et al. 2024), incorporating local ecological knowledge (LEK) may provide historical context and improve the effectiveness of management strategies, especially in regions with limited research resources, as demonstrated in studies of non-native blue crabs (*Callinectes sapidus* and *Portunus segnis*) in the Mediterranean (Marchessaux et al. 2023). This approach can provide detailed information across large geographic areas and on cross-ecosystem dynamics where traditional scientific monitoring may be limited (Langkilde et al. 2017).

Long-term monitoring is another critical aspect that is often overlooked. Although short-term studies provide immediate insights, extended research periods are essential for understanding the full effects of non-native species and may provide opportunities for before-and-after comparisons when invasions occur during the monitoring period. Similarly, modeling and simulation techniques can predict shifts in food webs and biodiversity under various invasion and management scenarios. Metacommunity models, for example, are useful for exploring complex interactions between ecosystems connected by non-native species.

The integration of machine learning and artificial intelligence into data analysis enhances the ability to process complex ecological datasets, model species distributions, predict invasion pathways, and identify key drivers of ecosystem change, providing powerful tools for managing and conserving affected ecosystems (Bjerge et al. 2023; Rakgoale and Ngetar 2024). For example, modeled predictions of non-native species spread could be used to develop monitoring protocols in ecosystems before invasion that target the variables most likely to be affected after invasion, especially in the case of microorganisms and pathogens (DeBruyn et al. 2025).

Conclusion

Based on the review of 143 articles and 212 case studies, it can be concluded that most studies on resource subsidies mediated by non-native species are relatively recent. Consequently, many studies do not provide a comprehensive overview of the long-term consequences of the role of non-native species in mediating resource subsidies. Most studies were conducted in North America and Europe, focusing primarily on reciprocal interactions between terrestrial and freshwater ecosystems. The most studied non-native taxonomic groups were plants, fish, and mammals, whereas the most affected native species were invertebrates, predominantly insects, and birds. The strong geographic bias observed inhibits a balanced understanding of the mediation of resource subsidies by non-native species, and further studies are needed, particularly in underrepresented but highly biodiverse regions of the world (Africa, Asia, and South America). Many ecosystem linkages remain understudied (e.g., freshwater–marine interactions) and require additional case studies to provide a clearer picture of the various mechanisms by which non-native species might exploit and mediate cross-ecosystem subsidies.

Collectively, these patterns suggest that much of the existing evidence reflects only a fraction of the biological invasion literature—one that is biased toward visible, charismatic, and economically relevant species in well-funded regions. As a result, the global network of biological invasions and resource subsidies remains only partially mapped, with many linkages among taxa, regions, and ecosystems insufficiently explored. Addressing these biases is essential for building a complete understanding of how biological invasions have altered and may alter energy and nutrient exchanges across ecosystem boundaries. Given these gaps, future research

priorities and techniques include long-term studies; the use of sensors, telemetry, environmental DNA, and metabarcoding techniques; the application of stable isotopes, fatty acids, and pollutants as tracers; and the integration of artificial intelligence and machine learning for handling large datasets.

Overall, this systematic review provides the first synthesis of resource subsidies mediated by non-native species and of how these species may add, reduce, and modify these subsidies in invaded ranges. By acting as vectors of energy, nutrients, and even contaminants across ecosystem boundaries, non-native species may expand their ecological footprint beyond the systems into which they are introduced. This raises the stakes for biodiversity conservation and ecosystem management, as non-native species may exert influence across broader spatial scales than previously recognized. Therefore, a framework that incorporates these cross-ecosystem flows provides a more complete basis for evaluating the impacts and costs of non-native species, identifying the network of stakeholders affected, and emphasizing the need to include such interactions in biological invasion impact assessments and management strategies.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

List of all case studies used in the revision

Authors: Letícia Alves, Janeide Padilha, Phillip J. Haubrock, Amanda Subalusky, Ronaldo Sousa

Data type: xlsx

Explanation note: List of all case studies used in the revision as requested by one of the referees

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