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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, having profound impacts on ecosystem functioning and affecting the provision of key ecosystem services. Despite the high number of studies on non-native species produced, mainly in the last two decades, one often overlooked aspect is their role as mediators of resource subsidies (i.e. cross-boundary movement of energy, nutrients, or materials). This topic may have theoretical and empirical applications since non-native species may play a major role in the connectivity of habitats transporting (or interrupting the transport of) energy and organic matter. Therefore, the main aims of this review were to (1) recognise main spatial, temporal, and taxonomic patterns and gaps in knowledge, (2) better understand how non-native species influence resource subsidies and their possible implications for ecosystem dynamics, and (3) identify future research avenues. Our review retrieved a total of 143 publications that matched our keyword search, resulting in a total of 212 case studies. These studies collectively show that non-native species can both disrupt and facilitate resource flows across ecosystem boundaries, with implications for ecosystem dynamics and connectivity. While terrestrial and freshwater connectivity accounted for the majority of published case studies (54%), many ecosystem linkages remain underexplored. A significant geographical 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 fish (25.5% of case studies) and mammals (21.7% of case studies), while important organisms such as fungi (0.9%) and bacteria (2.4%) were largely neglected, despite their fundamental role in decomposition processes. We identify key priorities for advancing this field, including long-term monitoring, the application of emerging molecular and analytical tools (e.g. telemetry, eDNA, metabarcoding, isotopic tracers), and the integration of artificial intelligence to synthesize large datasets. Our findings provide the first quantitative synthesis of resource subsidies mediated by non-native species, this information being crucial for biodiversity conservation and the effective management of ecosystems and their connectivity.

Keywords: biological invasions; connectivity; ecosystem functioning; management; meta-ecosystems; non-native species.

1. Introduction

Resource subsidies, defined as the cross-boundary movement of energy, nutrients, or materials, are central to the functioning of ecosystems (Polis, Anderson & Holt, 1997). These resources, originating in one habitat 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 & Post, 2019). These transferred resources are also termed spatial subsidies, or trophic subsidies (Polis, Anderson & Holt, 1997), and in this review, we will use the term resource subsidy throughout.

Despite the theoretical and management importance of resource subsidies to better understand the role of biodiversity and ecosystem functioning, terrestrial, freshwater, and marine ecosystems have largely been studied separately, probably as a response to historical isolation between 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, Thompson & Richardson, 2007; Marcarelli et al., 2011; Bartels et al., 2012; Subalusky & Post, 2019). For instance, adjacent food webs may be linked by cross-boundary subsidies, as seen in the reciprocal flows of invertebrate prey between streams and their adjacent riparian zones (Nakano & Murakami, 2001; Baxter, Fausch & Saunders, 2005). Terrestrial invertebrates can provide subsidies to freshwater organisms such as fish by falling into streams, while the emergence of adult aquatic insects can provide subsidies to riparian consumers such as spiders, birds and bats, establishing a reciprocal flux between both 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 high quantities of guano (Mulder, 2011), which can enhance the productivity of many terrestrial ecosystems (Wilder et al. 2022; Jones et al. 2025) and their surrounding coastal habitats, such as coral reefs (Savage, 2019; Benkwitt et al., 2022).

Most research on resource subsidies has focused on native species, particularly a few conspicuous taxa known to mediate strong cross-ecosystem flows, such as salmon during their spawning run, storm-driven seaweed, and arthropod emergence (Sato, Ueda & Takimoto, 2021). While numerous studies have examined non-native species and their ecological impacts (Andersen et al., 2004; Crowl et al., 2008; Pyšek et al., 2008; Mollot, Pantel & Romanuk, 2017), far less attention has been given to their role as mediator of such flows. This is although many non-native species can dramatically reshape community and ecosystem processes by introducing new subsidies or disrupting existing ones. Even though some studies 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 it challenging to study them. This has caused a gap in our understanding of the effects of non-native species on resource subsidies, potentially causing an underestimation of the breadth of their ecological impacts.

Recently, a study by Peller & Altermatt (2024) compiled some emerging examples that demonstrate the cross-ecosystem impacts of non-native species worldwide. However, that study also highlighted the need for a review collating 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, we conducted a review of studies examining resource subsidies affected by non-native species aiming to (*i*) recognize main spatial, temporal, and taxonomic patterns, biases and gaps in the existing literature, (*ii*) better understand how non-native species influence resource subsidies and their possible implications for ecosystem dynamics, and (*iii*) identify future research avenues. By systematically synthesizing this information, we provide the first comprehensive overview of invasion-affected resource subsidies, offering a foundation for future research and management of ecosystems and their connectivity.

2. Methods

A systematic approach was chosen because it ensures transparency and reproducibility while providing a comprehensive synthesis across taxa and ecosystems. A quantitative meta-analysis was not feasible due to the lack of standardized reporting of effect magnitude and subsidy measurements across studies, but a review allows us to identify taxonomic and geographic biases, synthesize evidence on resource subsidy pathways, and highlight critical knowledge gaps.

2.1 Bibliographical Search

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 keywords were employed: (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 to *Journals*, and the language to *English*. The search encompassed all articles up to the completion of the literature search on December 31, 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, 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, we recorded (i) the continent (Africa, Asia, Europe, North America, Oceania and South America) where the research was conducted, (ii) the publication year, (iii) the type of donor and recipient ecosystems (categorized into terrestrial, freshwater, and marine), (iv) the taxonomic group of the non-native species mediating the subsidy, (v) the taxonomic group of the affected native biota, (vi) the methodologies used, and (vii) the biotic and abiotic variables reported.

Taxonomic information was standardized and aggregated as Plantae, Algae, Actinopterygii, Mammalia, Aves, Arthropoda, Bivalvia, Amphibia, Reptilia. Unidentified or mixed taxa (e.g., Fungi, Bacteria, Microbes, and Invertebrates) were recorded as “Others”. Methodological categories were classified into controlled experiment, diet content analysis, DNA analysis, elemental analysis, field-based (field observation, field sampling and experiment) studies, modeling, remote sensing, stable isotope analysis, and field monitoring techniques (tagging, telemetry, and camera trap). When multiple methodological categories were applied within the same study, each was recorded separately, resulting in 212 total case studies. 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, temperature, and other environmental parameters. Variables grouped under other abiotic factors included light availability, nutrient concentrations, and hydrological characteristics. All percentages and frequencies presented in the results were calculated based on the total number of case studies (n = 212) (Figure 1).

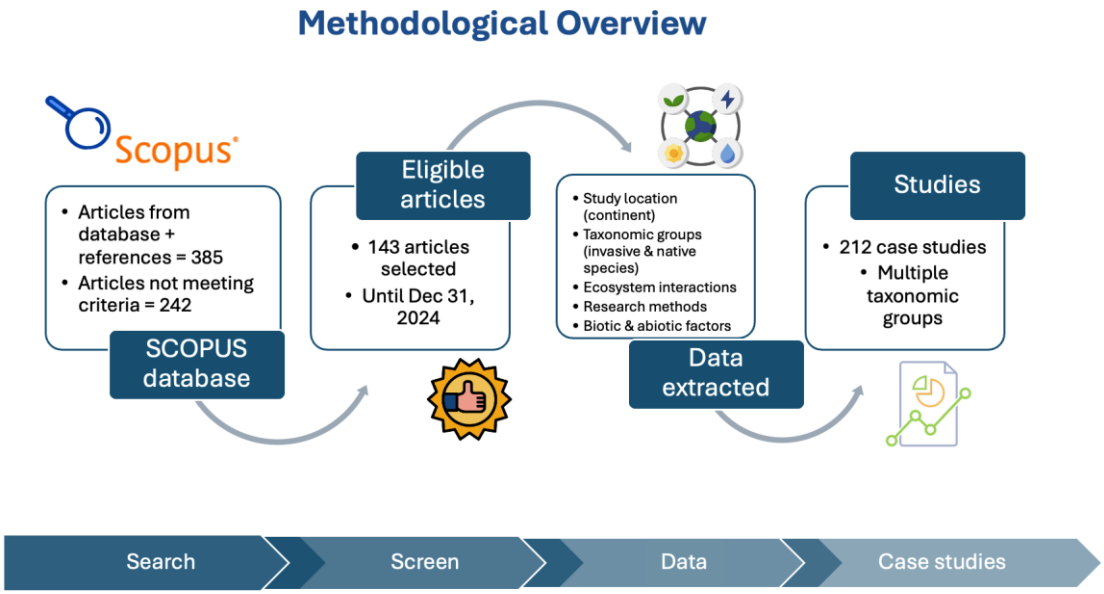

Figure 1. Flow chart of the review search, screening, data, and case studies.

2.2 Data Analysis

The collected data was processed using R Studio (R version 4.4.0; R Core Team, 2025). To visually highlight the results on the links between non-native and native species and the cross-ecosystem interactions, a flow chart was created using the R package `networkD3` (Allaire et al., 2017). The packages `rnaturalearth` (South & South, 2017) and `rnaturalearthdata` (South et al., 2017) were utilized to construct a map indicating the number of studies per continent.

3. General Patterns

3.1 Temporal distribution

While the number of publications on non-native species effects on resource subsidies identified by our literature search initially grew over time, it appears to have stagnated over the past decade. In fact, the number of papers increased rapidly from 2000–2004 to 2005–2009, peaking in 2010–2014 (Figure 2). However, there was a decline in publications from 2015–2019, followed by a very small resurgence in 2020–2024.

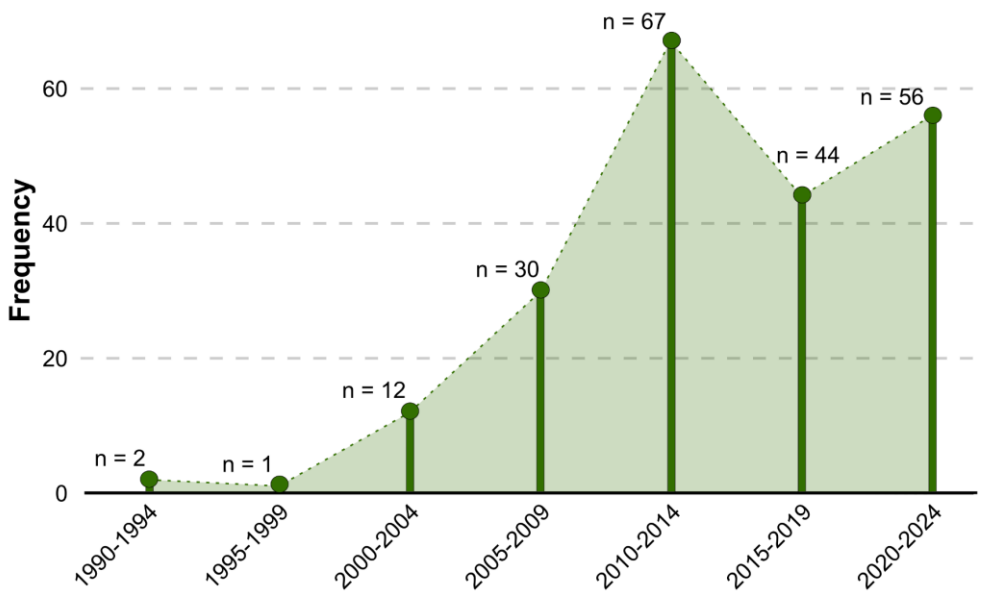

Figure 2. Number of publications produced per year on the topic of resource subsidies mediated by non-native species.

3.2 Spatial distribution

Most of the research on the effects of non-native species on resource subsidies originated from countries with high-income economies such as the United States of America (USA), Germany, and the United Kingdom (UK). North America dominates in research on resource subsidies mediated by non-native species (Figure 3). Europe ranks second in the number of articles produced, but with only a few countries (i.e., UK, Germany, France, Spain, and Portugal) represented. Similarly, most South American countries were not represented, with only some research conducted in Patagonia and Tierra del Fuego (Argentina and Chile). Although non-native species are well studied in Oceania, the topic of non-native species affecting the connectivity between habitats and ecosystems appears to be underrepresented, as there were only 12 studies identified. Also, for Asia, only a relatively small number of studies were identified (n = 11), with the majority originating from islands that are geographically located in Asia but politically aligned with countries from other continents, mainly the United Kingdom. Finally, we found only four studies published in Africa.

Despite the higher biodiversity present in the tropics, the vast majority of biological invasion literature 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 our data and also matches the hotspots of non-native species richness in countries such as the US and Australia (Turbelin *et al.*, 2017). However, studies such as Sekar *et al.* (2023) highlight the ecological significance of tropical and high-altitude ecosystems. These regions are largely underrepresented in our review yet increasingly subject to biological invasions (Zenni *et al.*, 2022).

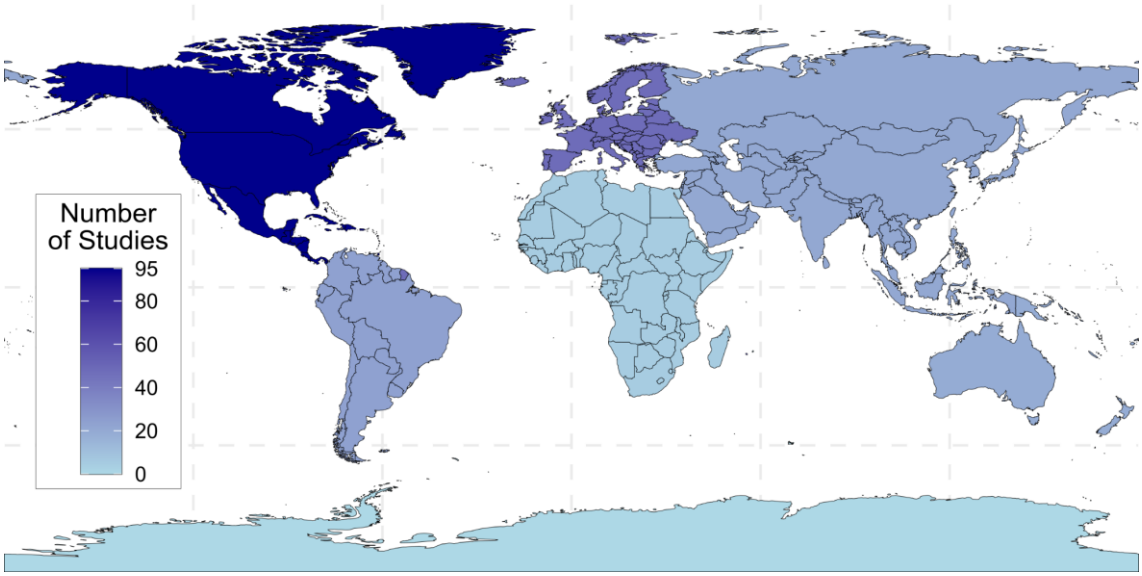

Figure 3. Number of publications published per continent on the topic of resource subsidies mediated by non-native species.

3.3 Methodological categories used

Field-based studies were the most commonly used technique (43%) (Figure 4). Examples include studies on introduced predators and temperature effects 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 (Owens *et al.*, 2023; Novais *et al.*, 2015; Novais, Pascoal & Sousa, 2017).

Stable isotope analysis was the second most widely used technique in the reviewed studies (17%). It has become an invaluable tool for reconstructing diets, characterizing trophic relationships, elucidating patterns of resource allocation, and constructing food webs. Consequently, the number of studies utilizing this method in trophic ecology has increased exponentially over the past decades (Boecklen *et al.*, 2011). Not surprisingly, stable isotope analysis was one of the most ubiquitous Methodological categories in the reviewed papers, as it enables quantitative estimates of the proportion of elemental fluxes across different trophic levels and habitats of a food web (Majdi *et al.*, 2018). Diet content analysis is another method widely used in trophic ecology (Winemiller, 1990; Majdi *et al.*, 2018) and was frequently present in studies examining the impacts of non-native species on native species across various habitats, given its accessibility and applicability at relatively large spatial and temporal scales.

Controlled experiments were employed in several studies (10%). 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. This approach enabled controlled manipulation of key environmental variables while retaining ecological realism, addressing the complex interplay between environmental conditions, human disturbance, and non-native fish establishment (Jackson *et al.*, 2013). Similarly frequent, elemental analysis was utilized in several studies (n = 8.5%), especially in case studies investigating the quality of subsidies provided by non-native plants and their transport to freshwater ecosystems (Kennedy & Hobbie, 2004; Lecerf *et al.*, 2007; Maerz, Cohen & Blossey, 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 only for a small percentage of studies, they can offer valuable complementary insights into species movement, behavior, spatial patterns, and stakeholder perspectives, 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 of resource transfers between habitats, often during unrelated fieldwork. For example, while conducting unrelated research, scientists observed an adult male red fox catching Common carp (*Cyprinus carpio*) along the shore, providing valuable insight into a novel mechanism of resource subsidy transfer (Tobajas & Díaz-Ruiz, 2022).

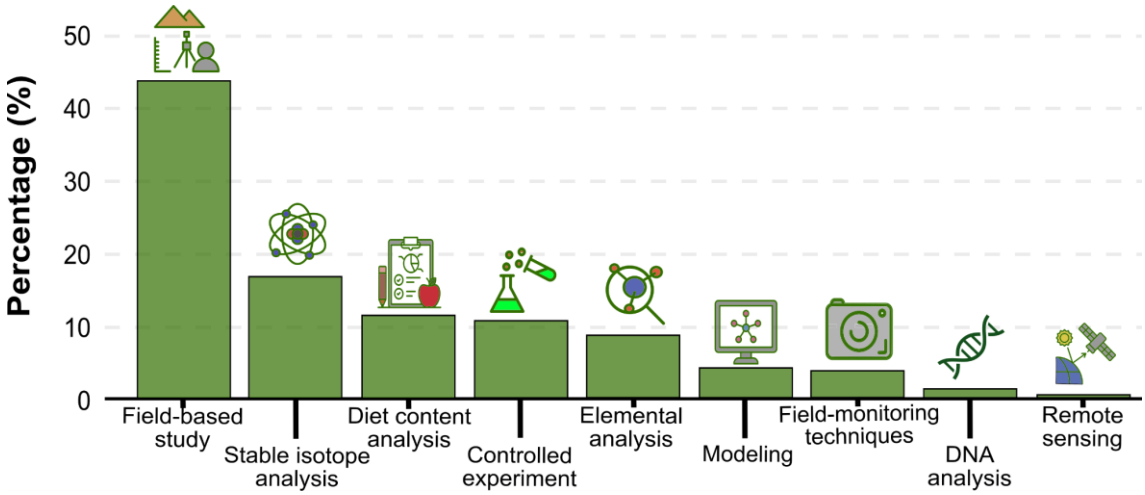

Figure 4. Percentage of methodological categories used in the 212 case studies analysed.

3.4 Biotic and abiotic factors measured

Many studies measure the impact on native species through various biotic parameters (n = 196) (Figure 5a). The most commonly assessed factors in impacted communities and species were biomass (26%), reflecting the focus on how non-native species alter energy flow or structural biomass within invaded ecosystems. These were 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) have also investigated factors that could influence the flow of subsidies between ecosystems and the effects of non-native species (Figure 5b). The most frequently measured variable was nutrient transfer (56.5%), especially carbon and nitrogen, which were directly associated with the impact of non-native species on cross-ecosystem subsidies. Organic compounds were assessed in 14 studies (16.5%), often related 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 is typically considered an indirect driver, influencing the magnitude or pathways of non-native species' impacts on resource subsidies rather than being directly altered by the species.

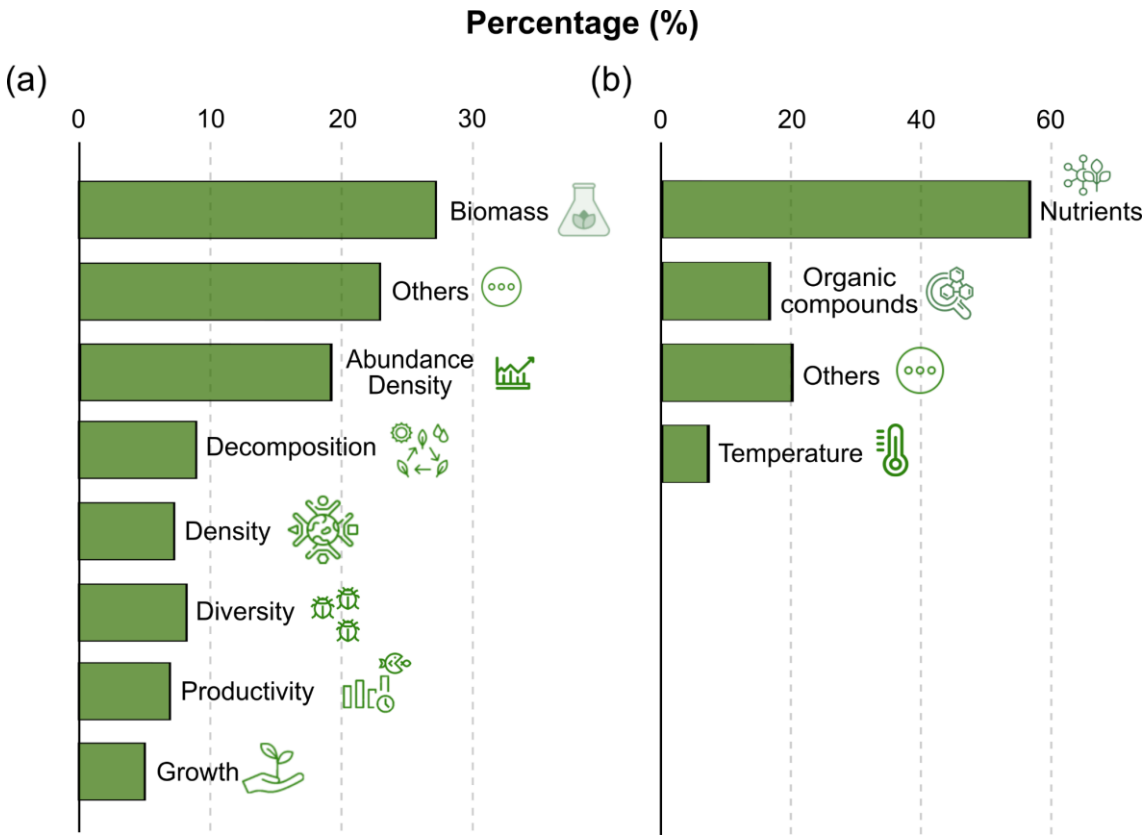

Figure 5. Percentage of case studies assessing different biotic (**a**) and abiotic factors (**b**).

3.5 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 (Figure 6). 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). In many studies (n = 37), mammals were identified as the group of non-native species threatening the highest number of species, particularly rodents (*Rattus spp.*) and feral cats (*Felis catus*), which primarily prey on birds (Dueñas *et al.*, 2021). Other notable groups, such as Arthropoda (mainly malacostracans [n = 14], with some cases focusing on insects [n = 6]), and Bivalvia (bivalves; n = 14), were central in several case studies. In contrast, the category Other included much 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, while 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 (Figure 6). The majority of documented interactions involved terrestrial–freshwater (36%) and freshwater–terrestrial (23%) linkages, while 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 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.

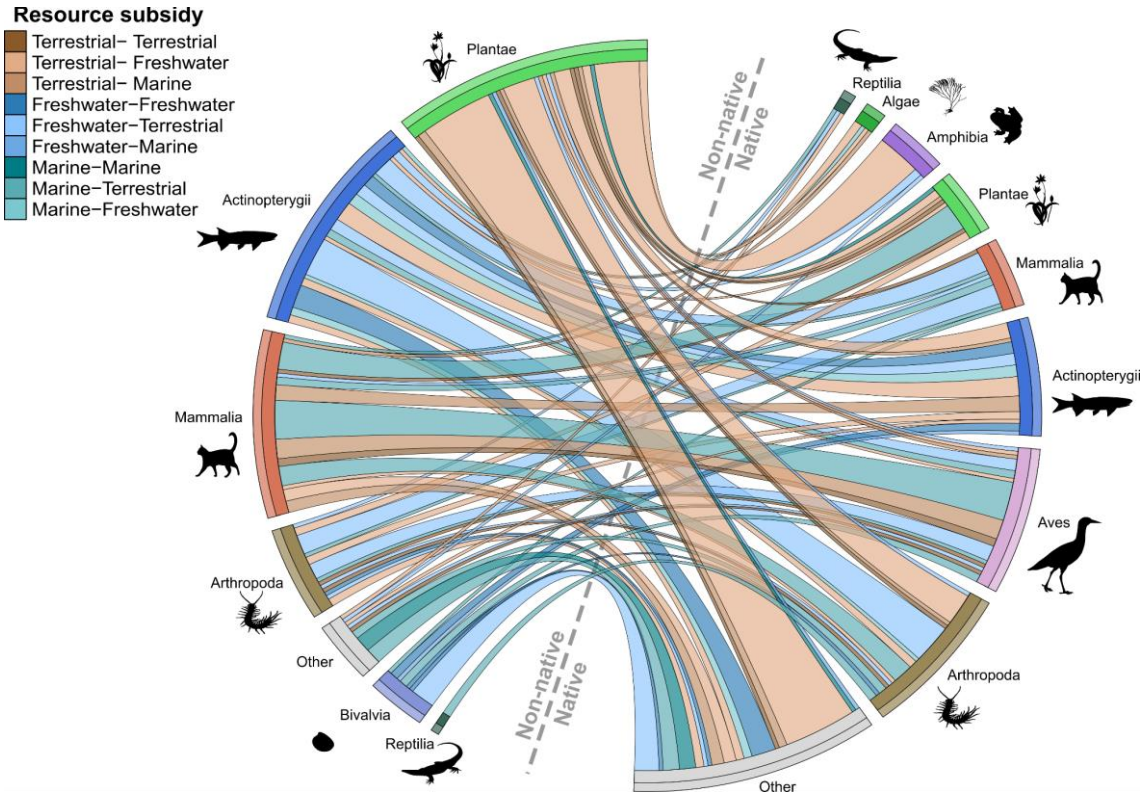

Figure 6. Sankey diagram showing the relationship between non-native taxonomic groups (left) affecting native taxa (right) through their direct and indirect effects on resource subsidies across different ecosystem linkages. Line thickness is proportional to the number of reported cases, illustrating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

4. 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. 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 were comparatively rare.

4.1 General Patterns

Terrestrial-Freshwater interactions emphasize the critical link between streams and riparian zones, widely recognized as interdependent systems, mainly connected by reciprocal flows of

invertebrate prey (Larsen, Muehlbauer & Marti, 2016). The reviewed publications predominantly examined Terrestrial-Freshwater interactions (33 %), which were studied across all continents. These studies are highly relevant, given the high biodiversity per 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 riparian non-native plants, which provide subsidies through litter production. Another important taxonomic group was Actinopterygii, where the primary mechanism was the predation of 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 in their aquatic larval stage, thereby interrupting their emergence as adults into terrestrial habitats. This disruption impacts riparian consumers and affects terrestrial food webs since 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, Knapp & Lawler, 2010; Jackson *et al.*, 2016).

Marine-Terrestrial interactions were the second most studied and were observed in almost all continents except Africa. Most of the links from Oceania originated from Marine-Terrestrial case studies. The primary taxonomic group responsible for these interactions was Mammalia, particularly non-native rats, which disrupt nutrient and guano flows from marine to terrestrial habitats by preying on seabirds (Pascoe *et al.*, 2022).

Some studies also focused on Terrestrial-Marine interactions, mainly conducted on North American and Asian islands. The primary processes driving these interactions were non-native rats preying on seabirds, reducing nutrient flow to coastal habitats, and the invasion of monocotyledonous plants, which reduced native tree abundance and, consequently, seabird abundance. This decrease in seabird abundance resulted in decreased nutrient transport to coastal ecosystems, reducing 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 habitats, providing nutrient subsidies to freshwater communities (Dunlop *et al.*, 2021; Muñoz *et al.*, 2021). On the opposite direction (i.e. freshwater-marine), we only retrieved one example concerning the die-off of the non-native Asian clam (*Corbicula fluminea*), where the soft tissues are consumed by the sea bass (*Dicentrarchus labrax*) in an Iberian estuary (Ilarri *et al.*, 2011).

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 habitats (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 estuarine non-native plants or algae on invertebrates (Taylor *et al.*, 2010; Krumhansl & Scheibling, 2012; Wang *et al.*, 2022). Another example of this interaction is by non-native bryozoans that may increase the amount of material eroded from subtidal kelp beds (*Saccharina longicruris* and *Laminaria digitata*), subsidising communities inhabiting deeper waters offshore (Krumhansl, Lee & Scheibling, 2011).

There were ten studies on Terrestrial-Terrestrial interactions. Examples include the 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, O'Dowd & Green, 2018). Some studies focused on more specific interactions, such as non-native feral pigs (*Sus scrofa*) that both displace native birds from foraging sites and facilitate access to food by disturbing the soil beneath nesting colonies of metallic starlings (*Aplonis metallica*) (Natusch *et al.*, 2017). Additionally, the presence of the non-native plant *Melaleuca quinquenervia* altered movement patterns of Florida panthers (*Puma concolor coryi*), by forcing panthers to move farther to access the habitat and resources they needed, creating novel spatial connections between ecosystems that were previously unlinked in the uninvaded area (Julian, Everham & Main, 2012).

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

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Species	Donor habitat	Recipient habitat	Description	Subsidy	References
Lymantria dispar	Terrestrial	Terrestrial	The non-native gypsy moth undergoes periodic outbreaks and represents a super-abundant food resource for predators, particularly native cuckoos (*Coccyzus erythropthalmus* and *C. americanus*).	Addition	(Barber, Marquis & Tori, 2008)
Melaleuca quinquenervia			In the presence of this non-native plant, panthers need to move farther to access the habitat and resources they need, creating a unique spatial flow connection between ecosystems that did not exist in the uninvaded state.	Addition	(Julian, Everham & Main, 2012)
Salvelinus fontinalis		Freshwater	Non-native brook trout consume many of the terrestrial invertebrate subsidies, reducing this resource for other species.	Disruption	(Rolla et al., 2018)
Lythrum salicaria			High floral density of non-native purple loosestrife increases adult dragonfly oviposition and subsequently high larval dragonfly abundance in the aquatic ecosystems.	Addition	(Burkle, Mihaljevic & Smith, 2012)
Rattus rattus		Marine	By depleting seabird populations, non-native rats disrupt the natural flow of nutrient subsidies (guano) to coral reefs, thereby reducing the biomass of coral reef fishes.	Disruption	(Benkwitt, Wilson & Graham, 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*) utilization of native forest coastlines.	Disruption	(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 offshore transport of nutrients and energy. As mussels reduce the availability of pelagic energy, fishes and invertebrates compensate by deriving more energy from alternative nearshore benthic or detrital energy channels.	Disruption	(Turschak et al., 2014)
Oncorhynchus spp.			In some introduced ranges, salmon forage in lakes and migrate to streams to spawn, connecting different freshwater habitats.	Addition	(Janetski et al., 2014)
Oncorhynchus mykiss and *Salmo trutta*		Terrestrial	Invaded sites decrease the availability of prey for riparian spiders that heavily rely on the emergence of insects.	Disruption	(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, a massive biomass of water hyacinth is moved from rivers to marine areas.	Addition	(Ronaldo Sousa, personal observation)
Corbicula fluminea			During *Corbicula fluminea* die-offs, their soft tissues are consumed by the sea bass *Dicentrarchus labrax*	Addition	(Ilarri et al., 2011)
Caulerpa taxifolia	Marine	Marine	Detritus from non-native algae subsidize invertebrate communities on intertidal mudflats.	Modification	(Bishop & Kelaher, 2013)
Codium fragile			Productive macroalgae can subsidize dense detritivore populations in the supralittoral, littoral or intertidal and deep benthic zones.	Modification	(Krumhansl & Scheibling, 2012)

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Alopex lagopus		Terrestrial	Arctic fox predation on seabirds reduces the nutrient subsidies from marine ecosystems. Impoverished soils affect the plant community.	Disruption	(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 predates sea lampreys during the migration from marine to freshwater ecosystems.	Disruption	(Boulêtreau et al., 2020)
Oncorhynchus tshawytscha			Anadromous non-native Pacific salmonids deposit great amounts of energy and nutrients of marine origin to rivers and lakes via reproductive products, excretion, and carcasses.	Addition	(Arismendi & Soto, 2012; Muñoz et al., 2021, 2022)

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4.2 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 (Table 2). 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 (Muñoz et al., 2022; Gerig et al., 2019; 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).

Novel prey introductions, 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 elevate predator populations and intensify pressure on native fauna (Simmons, Sterling & Watson, 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.

Table 2. Examples of non-native species providing novel resource subsidies, the mechanisms involved, and resulting ecological effects.

Mechanism / Type of Novel Subsidy	Non-native Species (Example)	Ecosystem Linkage	Key Effect(s)	Reference(s)
Marine nutrient transfer	*Oncorhynchus tshawytscha*	Marine → Freshwater	Adds marine-derived nutrients to oligotrophic streams; alters productivity and food webs	Muñoz et al. 2022
Contaminant transfer	*Oncorhynchus* spp.	Marine → Freshwater	Transports pollutants along with nutrients; affects recipient food webs	Gerig et al. 2019; Brandt et al. 2024
Carrion subsidies from mass mortalities	*Corbicula fluminea*	Freshwater ↔ Terrestrial	Provides organic pulses after die-offs; affects microbes, macroinvertebrates, and nutrient cycling	Novais et al. 2015, 2017; Sousa et al. 2012
Novel prey / trophic linkages	*Lepus europaeus*	Terrestrial ↔ Terr	Creates new predator competition (e.g. condor–eagle kleptoparasitism)	Perrig et al. 2023

		estrial		
Alternative prey subsidy	*Procyon lotor*	Marine ↔ Terrestrial	Increases raccoon density and predation on native prey	Simmons et al. 2014
Facilitation of resource access	*Sus scrofa*	Terrestrial ↔ Terrestrial	Exposes buried seeds and invertebrates; alters soil and bird foraging	Natusch et al. 2017
Outbreak-driven food pulse	*Lymantria dispar*	Terrestrial ↔ Terrestrial	Provides temporary food surplus for native cuckoos; alters migration and trophic impacts	Barber et al. 2008
Floral and fruit deposition	*Lythrum salicaria* and *Lonicera maackii*	Terrestrial → Aquatic	Increases organic input and insect activity; modifies aquatic communities	Burkle et al. 2012; Custer et al. 2017

4.3 Disruption or reduction of an already existent subsidy

Non-native species also disrupt or diminish existing resource subsidies, weakening cross-ecosystem connectivity through a variety of mechanisms (Table 3). 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 & Bugoni 2023). In riparian systems, the green alder sawfly (*Monsoma pulveratum*) and the European bird cherry (*Prunus padus*) reduce the supply of terrestrial invertebrate prey to streams, either through defoliation of native vegetation or replacement by less productive non-native plants (Roon et al. 2016; Roon, Wipfli & Kruse 2018). Direct predation by non-native fish and the amphipod *Dikerogammarus villosus* further suppresses the emergence or availability of aquatic insects, diminishing food for riparian predators such as spiders (Gergs et al. 2014; Jackson et al. 2016; Rolla et al. 2018). Behavioral disruption can also interrupt material flows, as shown by freshwater crocodiles (*Crocodylus johnstoni*) avoiding terrestrial foraging after poisoning by invasive cane toads (*Rhinella marina*), effectively severing aquatic–terrestrial energy transfer (Aiyer et al. 2022).

Table 3. Examples of non-native species disrupting or reducing existing resource subsidies and their ecological consequences.

Mechanism / Type of Disruption	**Non-native Species (Example)**	**Ecosystem Linkage Affected**	**Key Effect(s)**	**Reference(s)**

Predation on subsidy providers	*Rattus* spp. (rats)	Marine → Terrestrial	Reduces seabird colonies; interrupts nutrient transfer from marine guano to island soils	Linhares & Bugoni 2023
Defoliation of riparian vegetation	*Monsoma pulveratum* (green alder sawfly)	Terrestrial → Freshwater	Defoliates alder trees; reduces terrestrial invertebrate prey for juvenile salmon	Roon, Wipfli & Kruse 2018
Replacement of native vegetation	*Prunus padus* (European bird cherry)	Terrestrial → Freshwater	Supports less invertebrate biomass than native trees; weakens terrestrial prey subsidies to streams	Roon et al. 2016
Predation on subsidy flow	Non-native fish (various spp.	Terrestrial → Freshwater	Consume terrestrial invertebrates falling into streams, reducing food for native consumers (e.g. spiders)	Jackson et al. 2016; Rolla et al. 2018
Predation reducing emergent insect biomass	*Dikerogammarus villosus* (killer shrimp)	Freshwater → Terrestrial	Decreases aquatic insect emergence, reducing prey available for riparian spiders	Gergs et al. 2014
Behavioral alteration of native predators	*Rhinella marina* (cane toad)	Freshwater ↔ Terrestrial	Poisoning of crocodiles forces avoidance of terrestrial foraging, severing cross-ecosystem energy flow	Aiyer et al. 2022

4.4 Modification of subsidy

Another mechanism by which non-native species can alter the connection between habitats is through the modification of spatial subsidies. Instead of merely adding novel subsidies or interrupting subsidy flow, 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 compared to 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 in resource quality and palatability to consumers. This variation is often more dependent on resource quality and nutrient imbalances from 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, as differences in the quality of detritus produced by invading species compared to native species can impact tadpole performance, reducing subsidies to terrestrial consumers, and disrupting cross-ecosystem connectivity (Maerz *et al.*, 2010).

Similarly, the non-native bivalve *Corbicula 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, *Corbicula fluminea* has the

potential to profoundly affect organic matter dynamics and nutrient cycling in streams, impacting the linkage between the water column and benthic habitats (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 elevate local concentrations of dissolved nutrients via 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 & Flecker, 2013).

Another example is variations in the form of marine detritus (or wrack) washing up in coastal terrestrial ecosystems Different types of wrack deposits may not be uniformly utilized by invertebrates, as nutritional value can differ between 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.

5. Contextualization of findings

The synthesis of studies on resource subsidies mediated by non-native species revealed clear temporal, spatial, as well as taxonomic biases that shape the current understanding of cross-ecosystem processes. For instance, the total number of scientific publications has surged over the years, with the growth rate of newly published articles accelerating over time (Fire & Guestrin, 2019; WordsRated, 2023). Consistent with this global trend, publications on non-native species and habitat connectivity have also increased in recent years, although plateauing since 2014, reflecting their rising prominence in ecological and conservation research. This was notably onset by research activities that only began to increase in the early 2000s, coinciding with the broader rise of interest in trophic ecology and cross-ecosystem interactions (Polis *et al.*, 1997; Post, 2002). The recent deceleration in publication numbers may therefore partially reflect disruptions caused by the COVID-19 pandemic (Sloane *et al.*, 2021).

Geographically, North America and Europe dominated the published literature, while Africa, Asia, Oceania and South America remain underrepresented. This situation may reflect a much higher availability of funding opportunities and the concentration of research groups in the United States, where trophic studies have long been prioritized This imbalance may also partly arise from language constraints, as the review included only English-language publications, likely excluding relevant work published in Spanish, Portuguese, Russian, Chinese, among others (Angulo et al. 2021). This limitation (i.e. the search was limited to articles written in English, which might have introduced some bias) opens the possibility that the actual number of case studies on the mediation of subsidies by non-native species might be higher than reflected in this review, particularly in regions such as South America, Africa, and Asia. Oceania, however, presents a paradox: despite hosting some of the world's most threatened endemic faunas and facing severe non-native species impacts (Invasive Species Council, 2022), few studies have examined the connectivity between habitats mediated by invasions, highlighting a notable research gap. Given the limited number of studies conducted in tropical regions, there is a pressing need for more research that could provide important information and reveal broader patterns on the topic.

Taxonomically, most studies addressed only a small subset of taxa—typically those known to exert strong ecological or economic impacts (Thomsen et al. 2014). Mammals, particularly rodents (*Rattus spp.*) and feral cats (*Felis catus*), are disproportionately represented due to their well-documented roles in seabird colony collapse and nutrient disruption on islands (Wardle et al., 2009; Benkwitt, Wilson & Graham, 2020; Linhares & Bugoni, 2023). Similarly, beavers (*Castor canadensis*), introduced to Tierra del Fuego, receive attention because of their known ecosystem-engineering effects on terrestrial–freshwater connectivity (Henn, Anderson & Martínez Pastur, 2016). In aquatic environments, salmonid species dominate because of their dual status as ecosystem engineers and economically valuable fish in aquaculture and recreational fisheries (Vigliano et al., 2007; Dettmers, Goddard & Smith, 2012). Many studies conducted in South America mirror earlier research from salmonids' native ranges, illustrating how established research frameworks and funding priorities can shape global taxonomic distribution of invasion studies. Riparian plants such as *Lythrum salicaria* and *Prunus padus* have also received attention for their role in altering litter quality and nutrient inputs across terrestrial–freshwater boundaries, albeit to lesser extent (Mineau et al., 2012; Riedl, Clements & Pejchar, 2019).

Conversely, many taxonomic groups remain overlooked. Invertebrates, despite their ubiquity and importance as bioindicators, are often grouped generically and rarely resolved to class or order. Yet arthropods—especially riparian spiders and aquatic insects—play critical roles in connecting freshwater and terrestrial food webs, and their responses to invasion-driven disruptions are among the most direct (Jackson et al., 2016; Roon, Wipfli & Kruse, 2018). Amphibians are also underrepresented, despite their dual life cycles across aquatic and terrestrial realms. No studies were found on how chytrid fungus (*Batrachochytrium dendrobatidis*), a globally invasive pathogen, affects cross-ecosystem resource flows, though its severe mortality impacts likely disrupt both energy transfer and food-web stability (Capps et al., 2015; Fritz & Whiles, 2021; Zipkin et al., 2020). Likewise, microbial groups such as fungi and bacteria, fundamental to decomposition and nutrient cycling, 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).

Regarding ecosystem linkages, the dominance of terrestrial–freshwater pathways reflects the prevalence of research on riparian ecosystems, where bidirectional flows of nutrients, prey, and detritus are well documented, highlighting a strong geographic and taxonomic bias toward animal-mediated subsidies in temperate regions. On the other hand, it should be noted that we only retrieved one example of Freshwater-Marine interactions (i.e. Asian clam *C. fluminea* consumed by the sea bass *D. labrax*; Ilarri *et al.*, 2011). Although not published (or at least not retrieved in our review), other examples may exist and may encompass for example, the transport of water hyacinth (*Pontederia crassipes*) or the Brazilian waterweed (*Egeria densa*) from rivers to marine 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.

Collectively, these patterns suggest that much of the existing evidence reflects only a fraction of invasion science literature, one that is biased toward visible, charismatic, and economically relevant species in well-funded regions (Thomsen et al. 2014; Warren et al. 2017). As a result, the global network of biological invasions remains only partially mapped, with many linkages between taxa, regions, ecosystems, and habitats, and thus their resource subsidies, insufficiently explored. Addressing these biases becomes essential for building a complete

understanding of how biological invasions have and may alter energy and nutrient exchanges across ecosystem boundaries.

6. Invasions and resource subsidies: a meta-ecosystem view

As demonstrated above, non-native species can have a critical role in affecting resource subsidies across ecosystems. However, the impact of these subsidies depends on four key factors: quantity, quality, timing, and duration (following Subalusky & Post, 2019). Understanding these factors is vital for predicting and managing ecological outcomes of biological invasions in both natural and human-altered environments.

6.1 Quantity of Resource Subsidies

The amount of a resource subsidy that enters an ecosystem is one of the most straightforward but critical variables in determining its effect, and non-native species can clearly affect the quantity of prey, detritus or nutrients entering an ecosystem. Recognizing the limitations incurred from the lack of knowledge on resource subsidies of non-native species that can either bolster or destabilize ecological processes depending on the specific context underscores the need for a broader, integrative framework—one that explicitly considers cross-ecosystem processes and feedbacks at larger spatial and temporal scales.

In systems where nutrient availability is naturally limited, a sudden increase in resource input by non-native species can stimulate primary productivity, leading to higher biomass and an increase in 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 the availability of nitrogen in invaded ecosystems, serving as a significant N source for benthic primary producers, potentially driving bottom-up changes in the food web. By displacing particulate organic matter and macroalgae as the primary food source for lower-level consumers, albizia also indirectly provides carbon (C) and nitrogen (N) to higher-level consumers (Atwood *et al.*, 2010). Taylor *et al.* (2010) found that the quantity of detritus from non-native *Caulerpa taxifolia* had a stronger impact than its initial quality, 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, the overloading of nutrients can result in eutrophication, where excessive algal growth depletes oxygen in the water, which may be detrimental for most aquatic life. This situation has been described in response to massive 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, Finn & Franz, 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, and this is a future research avenue that should be explored.

6.2 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, while 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 habitats, impacting various organisms, such as *Daphnia* and developing anuran larvae (Griffiths *et al.*, 2021; Diller *et al.*, 2022, 2023; Iglesias-Carrasco, Cabido & Ord, 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 like 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 non-native *Impatiens glandulifera*, with its high leaf nitrogen content, supported the highest densities and richness of macroinvertebrates. This suggests that consumer communities gather around the highest-quality litter, accelerating litter breakdown rates regardless of whether the source is native or non-native. Similarly, Stephens, Berven & Tiegs (2013) found that three non-native wetland plant species provided conditions for the development of amphibian metamorphs that were heavier, had shorter larval periods, and showed higher survival rates compared to those from native wetland 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 boost 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, organic matter that is difficult to decompose, such as lignin-rich materials from certain non-native plant species, such as water hyacinth that move from rivers into marine ecosystems during floods (Ronaldo Sousa, personal observation), may alter decomposition rates and nutrient cycling processes. The impact of subsidy quality is also linked to the adaptability of the organisms in the recipient ecosystem. Some species can capitalize on low-quality or novel resources, while others may be disadvantaged, leading to shifts in species composition and ecosystem functioning. The process of invasion can be highly amenable to assessing this situation, but we are not aware of any study addressing this topic.

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 range, as in several regions of South America, they may act as invasion-mediated contaminant transfers. This remains largely unexplored and warrants further investigation due to potential impacts on native biodiversity and ecosystem functioning (Brandt *et al*., 2024).

6.3 Timing of Resource Subsidies

The timing of resource subsidies can have profound effects on how they are integrated into ecosystems and 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 for possible consumers; an issue that remains unexplored and needs further research.

For instance, in many systems, resource subsidies arrive in predictable seasonal pulses, which 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 capitalized upon 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).

6.4 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, while others are more chronic, continuously influencing ecosystem dynamics over extended periods. Few studies address this subsidy characteristic, but for example, Novais *et al.* (2015, 2016) assess the possible effect of non-native clams on terrestrial ecosystems through time, with clear temporal changes in some nutrients and the microbial and macroinvertebrate communities. However, it is possible that the legacy of effects could be extended for more than 3 months (the duration of the study), and for example, terrestrial plants may respond to this resource subsidy in a much longer time 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 in sustaining populations during otherwise resource-scarce times. A clear example is the introduced Pacific salmon (*Oncorhynchus* spp.), which provides 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 the trout's 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 & 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. However, at high detrital loads,

macroinvertebrate diversity declined, likely due to sediment hypoxia induced by excessive organic matter.

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 the dynamics of ecosystems across the globe. While subsidies can enhance productivity, support biodiversity, and maintain ecosystem functions, their effects are highly context-dependent because the habitat characteristics may also play a significant role on 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, 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 effect on recipient ecosystems if 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 establish, with impacts cascading into connected habitats and expanding the range of stakeholders affected. Considering these complex interactions allows ecologists and policymakers to better predict ecological responses and to develop management strategies that promote ecosystem resilience and sustainability in the face of biological invasions.

7. Future directions

The study of trophic ecology is evolving rapidly. As technology improves, new tools and methodologies will be developed and applied to advance new research and to enhance our 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. Advancements in sensor technology and telemetry allow scientists to track movements and behaviors, even in small organisms, with great accuracy, allowing researchers to study the spatial dynamics of non-native species and their role in mediating resource subsidies (Meira, Byers & Sousa, 2024; Ellis-Soto *et al.*, 2021). Innovative approaches like bioacoustics could also offer a more profound insight on the ecological impacts of non-native species (see Meira *et al.*, 2024b). Studying changes in acoustic interactions within and between ecosystems may thus reveal shifts in species communication and behavior, potentially indicating broader shifts in ecosystem dynamics. Molecular techniques like metabarcoding and environmental DNA (eDNA) analysis are also revolutionizing the detection and monitoring of non-native species across different habitats (Westfall, Therriault & Abbott, 2020). Future applications should move beyond detection toward quantifying trophic linkages and tracing resource flows. Combining molecular tools with biochemical tracers like fatty acids and stable isotopes will enable finer resolution 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). In a similar fashion, some pollutants could be used as tracers to assess the role of non-native species as resource subsidies (Brandt *et al.*, 2024; Twining *et al.*, 2025).

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

Long-term monitoring is another critical aspect often overlooked. While short-term studies provide immediate insights, extended research periods are essential for understanding the full effects caused by non-native species, and may provide the opportunity for before-after comparisons when invasions occur during the period of monitoring. 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 habitats connected by non-native species.

The integration of machine learning and artificial intelligence in 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 & Ngetar, 2024). For example, modeled predictions of non-native species spread could be used to develop monitoring protocols in the ecosystem prior to invasion that could target measures most likely to be impacted post invasion, especially in the case of microorganisms and pathogens (DeBruyn *et al.*, 2025).

Future research should also address the role of microorganisms, particularly fungi, bacteria, and viruses, in mediating resource subsidies (Marcarelli *et al.*, 2011; Metcalf *et al.*, 2016; Bahram & Netherway, 2022; DeBruyn *et al.*, 2025). The lack of case studies displaying these groups reflects an incomplete understanding of their ecological impact and the mechanisms driving their invasions. As fungi and bacteria play crucial roles in decomposition and nutrient cycling, they are likely among the first organisms affected by shifts in resource subsidies. However, very few studies assess the effects of subsidies mediated by non-native species on these important organisms.

8. Conclusions

Through 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 mediating resource subsidies. Most studies were conducted in North America and Europe, focusing primarily on terrestrial and freshwater reciprocal interactions. The most studied non-native taxonomic groups were fish and mammals, while the most affected native species were invertebrates, predominantly insects. The strong geographical bias observed inhibits a balanced understanding of the mediation of resource subsidies by non-native species, and more studies need to be performed, 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. Given these gaps, future research directions and techniques include the need for long-term studies; the need to incorporate a meta-ecosystem perspective in future 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 review provides the first quantitative synthesis of resource subsidies mediated by non-native species, and how these species may add, disrupt, and modify these subsidies in the invaded range. Non-native species acting as vectors for energy, nutrients, and even contaminants across ecosystem boundaries, may expand their ecological "footprint" beyond the systems in which they are introduced. This raises the stakes for biodiversity conservation and ecosystem management, as non-native species may exert influence over broader spatial scales than previously recognized. Therefore, a meta-ecosystem perspective that incorporates these cross-ecosystem flows provides a more complete framework for evaluating non-native species impacts and costs, 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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