

Monograph

Marine amphipods as integral members of global ocean ecosystems

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ABSTRACT

Amphipod crustaceans exist across marine habitats from the polar regions to the tropics, providing a critical biological link between benthic/pelagic processes and marine/atmospheric ecosystems. They fulfil many functional roles as predators and prey, bioturbators, mesograzers, pollinators, secondary producers, nutrient cycling facilitators, and indicators of marine and sediment health. Despite their importance, tropical amphipods are poorly represented in the literature. This review offers an overview of the biological and ecological roles of amphipods globally. Amphipods face many pressures in the warming seas that will ultimately force acclimation, adaptation, or mortality, with potentially dire consequences for the processes they facilitate. We highlight the lack of data on tropical amphipods and argue an urgent need to identify their diversity, abundance, and functions underpinning resilience in ecosystems such as coral reefs, seagrass meadows, and mangroves. This improved understanding is necessary to predict and potentially mitigate cascading deleterious effects driven by a rapidly warming planet.

1. Introduction

The order Amphipoda consists of seven accepted suborders, six of which are found in marine environments: Amphilochidea, Colomastigidea, Hyperiidea, Hyperiopsidea, Senticaudata, and temporarily named Amphipoda *incertae sedis* (WoRMS, 2023). Currently, 10,590 amphipod species are recognized in marine, brackish, freshwater, and terrestrial environments, with approximately 79% of these considered marine dwelling species (WoRMS, 2023). It is estimated that only one third of amphipod species in existence have been described to date across all habitats (marine, brackish, freshwater, terrestrial) based on the rate of amphipod species discovery since their first descriptions in the mid-1700s (Arfianti et al., 2018) (Fig. 1). Although body plans may differ between groups (Fig. 2), these crustaceans generally have bilaterally symmetrical, compressed, and segmented bodies containing a cephalon, a pereon, and a pleon (Fig. 2A), and most species exhibit sexual dimorphism (Conlan, 1991). Walking legs (pereonites) and swimming legs (pleonites) afford amphipods high mobility. Amphipods are found from the intertidal flats to the deep sea and may range in size from 500 µm to 340 mm, with larger specimens located in colder or hadal environments (see Li et al., 2019). Diets vary between species; marine amphipods may be herbivores, carnivores, filter feeders, detritivores, or scavengers, though some exhibit a combination of feeding behaviours.

Amphipods perform critical roles in marine environments, yet they are often overlooked and under-appreciated for their contribution to ecosystem function, particularly in tropical ecosystems (Figs. 3 & 4). Indeed, the biological and ecological roles of amphipods are generally acknowledged as being under-valued and understudied (Conlan, 1994; Arfianti et al., 2018). Most studies have predominantly investigated their role as a food source for higher organisms, their use as toxicity and pollution indicators in water or sediment (Dauvin, 2018), and their spread as invasive species (Bhoi et al., 2023) (Fig. 4). However, amphipod functional traits and importance to various habitats extend beyond these basic descriptions of their biology or utility in toxicity testing (which is not the focus of this current review). These crustaceans are also recognized as bioengineers (Howard and Dörjes, 1972), benthic-pelagic coupling facilitators (Limia and Raffaelli, 1997; Dauby et al., 2003), and widespread mesograzers (Howard, 1982; Buschmann and Santelices, 1987; Berthelsen and Taylor, 2014). Amphipods live everywhere between the coastal shallows and the deep sea (Ahyong and Hughes, 2016), and thus, more comprehensive knowledge of their biology and ecology would provide a better understanding of the inner workings of ecosystems throughout the ocean.

A rapidly changing global climate is resulting in increased marine heatwaves, ocean acidification, and eutrophication, leading to concerning declines in sensitive marine ecosystems worldwide (e.g., Hobbs

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and McDonald, 2010; Guan et al., 2020; Plaisted et al., 2022). Marine conservation and research efforts are predominantly focused on commercially relevant species (e.g., fish), charismatic megafauna (turtles, sharks, whales) or ecosystem builders (corals), though as ecosystem impacts become more extreme, the unseen majority, including amphipods, are likely equally impacted. Many studies on amphipods investigate these organisms in polar or temperate regions, leaving extensive knowledge gaps of their roles in tropical ecosystems and specifically tropical coral reef, mangrove, and seagrass habitats, all of which are highly vulnerable to increased stressors. The ability of these animals to cope with stress and acclimate or adapt to rapidly changing environmental conditions will be critical in underpinning the continuing function and resilience of ecosystems worldwide. Here we provide a comprehensive review of the importance of amphipods within various marine ecosystems, highlighting their ecological significance and their sensitivity to environmental change, and revealing how their loss would deeply impact surrounding biotic and abiotic areas. We also highlight the paucity of knowledge of amphipod biology and ecology in tropical coral reef, mangrove, and seagrass ecosystems, detailing how increased research effort is needed on these cryptic crustaceans to aid in the preservation of critical tropical habitats faced with an increasingly uncertain future.

2. Marine amphipods contribute to ecosystem function

2.1. Benthic and pelagic connective relationships

Amphipods provide a critical link between trophic levels (Fig. 3). As important secondary producers around the globe, their abundance influences the success of a multitude of other animals within marine ecosystems. In the polar regions for example, an average of 60 million tonnes of sympagic amphipods are consumed annually, contributing more to bird, fish, and mammal diets than any other creature besides krill (Dauby et al., 2003). These amphipods provide both direct and indirect links between the algae growing in the ice upon which they feed and the larger animals in the sea and sky that ingest them (Bard, 1999; Acha et al., 2015). The polar amphipods are high in polyunsaturated fatty acid and overall lipid content (Auel et al., 2002; Graeve and

Greenacre, 2020; Bhoi et al., 2023), making them highly nutritious options for seabirds such as auks, prions, murre, and penguins (Ainley et al., 1992; Bost et al., 1994; Weslawski et al., 1994; Croxall et al., 1999; Chardine, 2001; Elliott et al., 2008); harp, ringed, and bearded seals (Bluhm and Gradinger, 2008); squid (Smetacek et al., 2004); whales (Oliver and Slattery, 1985; Grebmeier and Harrison, 1992; Dunham and Duffus, 2002; Bluhm and Gradinger, 2008); and walrus (Fay, 1982).

Studies from lower latitudes have similarly confirmed the importance of amphipods as prey items for a range of fish including commercially relevant species such as cod (Dalpadado, 2001; Gradinger and Bluhm, 2004; Dalpadado et al., 2016), yellowfin sole (Black et al., 2013), salmon (Chang and Parsons, 1975; Daly et al., 2010; Duffy et al., 2010), and flounder (Franz and Tanacredi, 1992; Cattrijsse and Hampel, 2006). Notably, 80% of Atlantic spiny lumpfishes collected in one study had solely amphipods in their stomachs (Berge and Nahrang, 2013), and a survey of all fish along the North-East shelf of the United States identified amphipods as one of the top ten most consumed prey items (Smith and Link, 2010). Inhabitants of coastal habitats such as marshes, seagrass beds, and coral reefs also frequently ingest amphipods. For example, the salt marsh crab *Armases cinereum*, isopods, and shrimp regularly consume amphipods (Ejdung and Elmgren, 2001; Buck et al., 2003; Fry et al., 2003), as do multiple species of skates along the shoreline (McEachran et al., 1976; Ebert and Bizzarro, 2009; Barbini et al., 2010). Smaller coastal fish such as mummichogs (Graham et al., 1998; Deegan et al., 2007), reef fish (Choat and Kingett, 1982; Denny and Schiel, 2001), and rocky or soft bottom associated fish assemblages (Stål et al., 2007) also commonly ingest amphipods. While there is evidence of tropical fish predation on amphipods on reefs (Choat and Kingett, 1982; Russo, 1991), mangroves (Hajisamiae et al., 2003), and seagrass beds (Kwak et al., 2015) around the globe, there has been little research on the role of amphipod abundance in structuring the surrounding fauna, though it has been acknowledged that cryptic fauna such as amphipods likely play an important yet unrecognised role in tropical trophic webs (Tebbett et al., 2023). Overall, amphipods are critical in all globally important marine ecosystems through supporting and connecting trophic levels, but their specific roles and influence in tropical habitats largely remain to be described.

In addition to their role as prey, amphipods have occasionally been

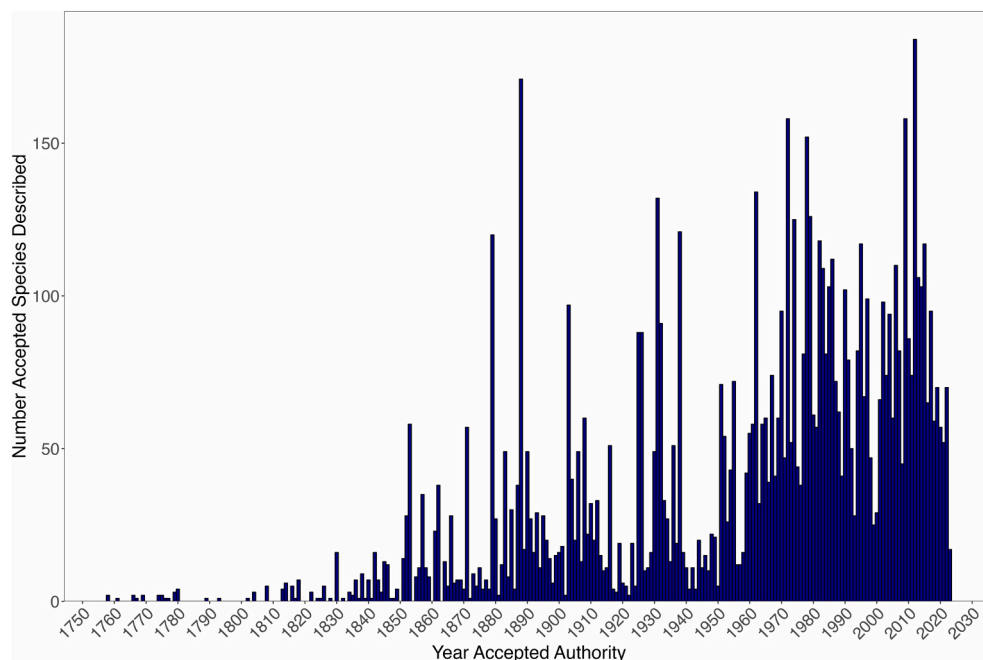


Fig. 1. Annual number of new amphipod species described based on date of manuscript. Only currently accepted species names were included. Data procured from the World Register of Marine Species database (July 2023).

termed “keystone species” within benthic faunal communities (Bobsien, 2006; (Smith et al., 2014); Chen et al., 2021). In fact, the presence of mesograzers alone may be enough to structure both overall invertebrate and algal assemblages in fouling communities through direct and indirect effects of consumption (Duffy and Harvilicz, 2001). Their ability to rapidly colonise foraging pits of whales and rays, or other similarly disturbed benthic areas, ensures that fish and other life returns to perturbed sections of substrate (Oliver and Slattery, 1985; Bonsdorff and Blomqvist, 1993; Cross and Curran, 2004). Further, some amphipod species (e.g., *Marinogammarus marinus*; suborder Senticaudata) are predators themselves, exerting pressure and direct control over other small crustaceans and zooplankton (Dick et al., 2005; Bobsien, 2006; Alexander et al., 2012). Even in the deepest parts of the oceans, characterized by extreme conditions of complete darkness, low temperatures, high pressures and limited food sources, amphipods constitute the predominant (>95%) diet for hadal liparids, providing these deepest known fish with highly nutritious chitinous exoskeletons and interior gut contents (Gerringer et al., 2017; Tokuda et al., 2020). Importantly, amphipods in these deep habitats are a critical link in the oceanic carbon cycle, sourcing their own diets from sinking labile organic matter from the surface waters, thus providing efficient nutrient recycling through complex trophic food chains (Wang et al., 2019).

2.2. Parasitism

Some species of amphipods engage in parasitism, especially those from the infraorder Lysianassida (suborder: Amphilochidea) (though this is not exclusive to this group; Vader, 1970, Gooday, 1984). Lysianassid amphipods generally live in deep, cold seas and have been observed attacking foraminifers (Gooday, 1984), brachiopods (Vader, 1970), and fish (Hannah et al., 2012). Some hyperiid amphipods also seem to parasitize scyphozoans (Riascos et al., 2012; Lafferty, 2013), though the relationship has been suggested to be more so one of predation than parasitism (Johnson et al., 2001). Although fish tend to struggle during jellyfish outbreaks, the increased number of amphipods parasitizing the jellyfish are suspected to provide an increased source of

food for fish stocks (Riascos et al., 2012). Amphipods from the Cyamidae family (suborder: Senticaudata) offer the clearest examples of parasitism, as they feed on the flesh of larger organisms such as whales (Poulin and Hamilton, 1995) and hence are commonly called “whale lice.” Though some families of amphipods in the tropics are suspected to be parasitic, most evidence of this behaviour is circumstantial at best with isolated observations of supposed parasitism mentioned only in passing (e.g., in Gershwin, 2006), and further exploration is necessary to understand their roles in warmer habitats.

2.3. Bioturbation and other substrate interactions

Some amphipod species indirectly influence benthic faunal assemblages through their interactions with the substrate. Many amphipods build tubes or burrows to live in, creating microheterogeneity in substrate structure (Burd et al., 2008). For example, the complex mat of tubes formed by *Haploops nirae* amphipods (suborder: Amphilochidea) defines the entire area populated by this species, increases adjacent species richness, and maintains a relatively unique assemblage of associated benthic macrofauna drawn to the uneven substrate (Rigolet et al., 2014). Burrowing amphipods such as those from the Corophiidae family (Fig. 2C; suborder: Senticaudata) also impact surrounding meiofaunal communities and increase other species' abundances because of the freshly oxygenated and enriched sediment surrounding the burrows (Limia and Raffaelli, 1997).

Such crypto-bioturbation alters sediment chemistry and can increase sediment suspension in the water column (Dashtgard and Gingras, 2012). Though the reworking of the substrate may be on a small scale relative to the ecosystem occupied, studies have indicated disproportionately large cascading effects of the disturbed sediment mixing in the water column, including nutrient release into the localised area and increased rates of benthos turnover (Howard and Dörjes, 1972; Grant, 1983). Foraging behaviours of larger animals such as rays and whales searching the substrate for amphipods and other food amplifies the extent of this substrate mixing as well, and the combination of these processes de-stratifies the water column (Dashtgard and Gingras, 2012;

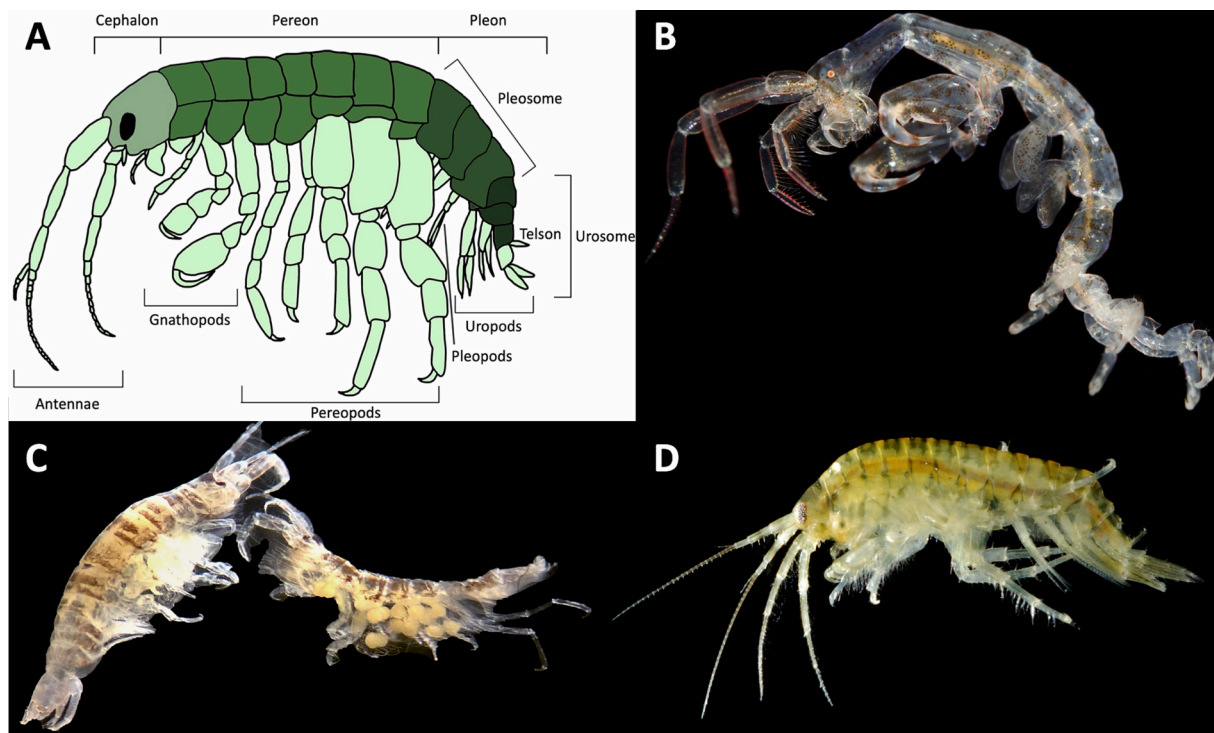


Fig. 2. (A) Generalized body plan of a gammaridean amphipod, (B) *Caprella equilibra*, (C) family Corophiidae, and (D) *Gammarus tigrinus*.

Howard and Dörjes, 1972). If chemicals or other pollutants are present in the sediment, this bioturbation may increase the toxic load in the water column (Burton and Johnston, 2010).

Additionally, tube-building amphipods may facilitate denitrification microbial processes in the substrate during the tube-making process (Pelegri and Blackburn, 1994), which hastens nutrient cycling and availability to other organisms. In coastal areas, these disturbances also reduce the stability of the sediment (Allen and Moore, 1987), which can expedite the advancement of coastal erosion and create challenges for intertidal plants. For example, *Corophium volutator* (suborder: Senticaudata) amphipods feeding on diatoms along the shoreline of the Bay of Fundy would readily destabilise the area if their population was not kept in check by local shorebirds (Boogert et al., 2006). Conversely however, another study found that burrowing and tube-building amphipods reduce the sediment availability for transport and erosion in a coastal habitat (Grant and Daborn, 1994), potentially indicating that the relationship between amphipods and their benthic zones may differ depending on the substrate type.

2.4. Scavengers and detritivores

Beyond structural alterations to the benthos, marine amphipods are well documented scavengers and detritivores on the seafloor (Fig. 3). Several studies have identified amphipods as one of the most important animal groups interacting with organic litter and recycling organic matter in a variety of habitats (Hessler et al., 1978; Bosire et al., 2005; Castro et al., 2005). Deep sea amphipods in particular form crucial links between both horizontally and vertically distinct marine habitats due to their voracious feeding behaviours. In abyssal (4000–6000 m) and hadal (6000–11,000 m) zones once thought to be devoid of life, amphipods have evolved diverse adaptations to thrive in such inhospitable environments, and they are recognized as the primary scavengers of hadal trench zones (Blankenship and Levin, 2007). When prompted by olfactory cues triggered by the scent of death, deep sea lysianassid amphipods are able to internally produce increased levels of oxygen (Thurston,

1979; Smith and Baldwin, 1982; Premke et al., 2006). These unique adaptations allow them to swim great distances rapidly before eating all but the bones of marine carcasses, thus facilitating nutrient cycling and gene flow across the benthos (Havermans and Smetacek, 2018).

In general, significantly more amphipods have been documented in patches of debris (i.e., detritus, shells, wood chips) than bare patches (Oliver and Slattery, 1985), completing the complex web of trophic interactions by clearing the seafloor and releasing nutrients back into the environment (Fig. 3). Benthos-associated and deep sea amphipods may be niche or generalist feeders due to their high diversity (Havermans and Smetacek, 2018), but all connect the depths to the shallows via consumption of decaying animal and plant material in addition to assimilation of other labile organic matter (Wang et al., 2019).

2.5. Amphipods impact marine plant and algal communities

Though multiple amphipod species are detritivores and scavengers, many others are omnivores and herbivores that are known to consume plants and algae. In arctic sea ice, amphipods comprise >90% of under-ice macroinvertebrates and graze heavily on sympagic algae, which in turn drives larger animals to ice edges to feed on the amphipods (Cross, 1982). In areas where multiple macroalgae species occur, some amphipods may have distinct dietary preferences (Dean and Connell, 1987; Arrontes, 1999; Taylor and Brown, 2006; Buza Jacobucci and Pereira Leite, 2014); thus, the effect that amphipod grazing has on plants and algae varies greatly depending on the species involved (Duffy, 1990). High macroalgal diversity has been observed in some coastal regions (Fredriksen et al., 2005), and this diversity may increase the number of preferentially grazing amphipod species that support greater overall species richness in the community (Duffy and Harvilicz, 2001).

In seagrass habitats, amphipod abundance may be a suitable indicator of seagrass degradation and habitat health (Carvalho et al., 2006). Here, grazing effectively maintains the balance between epiphytes and grasses by preventing overlaid blades from collapse and encouraging healthy plants, higher primary production through photosynthesis, and

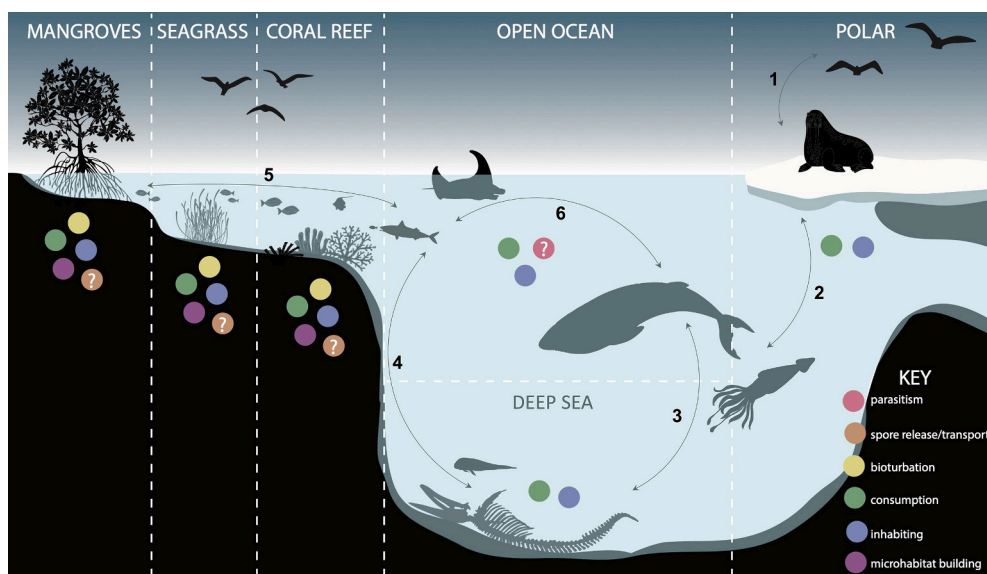


Fig. 3. The confirmed and predicted ecological roles and trophic interactions of marine amphipods across mangrove, seagrass, coral reef, open ocean, deep sea, and polar habitats. The ecological roles within each habitat are represented by coloured dots. Solid dots indicate confirmed roles or behaviours; dots with a question mark indicate suspected roles or behaviours. Arrows indicate simplified trophic pathways through which amphipods support marine ecosystem processes: 1- sympagic amphipods are ingested by seabirds and ice-dwelling animals; 2- sympagic amphipods support abundant fish populations, which are ingested by squid, whales, and other vertically migratory species; 3- sinking organic matter derived from microbes, plants, and pelagic animals, (e.g., whalefall and other marine carcasses) supports deep sea vertebrate and invertebrate populations; 4- amphipods provide food for hadal fish, which contributes to recycling nutrients from the depths back into the surface waters of the oceans through complex trophic food webs; 5- amphipods ingested by numerous vertebrate and invertebrate species in shallow nearshore habitats support coastal food webs; 6- pelagic animal species are dependent on healthy food webs that are intrinsically connected to coastal processes and deep ocean ecosystems, all underpinned by amphipods.

increased nitrogen availability from decaying plant matter (Robertson and Mann, 1980; Howard, 1982; Orth and Van Montfrans, 1984; D'Antonio, 1985; Hall and Bell, 1988; Berthelsen and Taylor, 2014; Michel et al., 2020). Additionally, high densities of amphipods may mitigate periodic algal blooms in the water column via consumption (Andersson et al., 2009). Decreased amphipod abundances in seagrass meadows have resulted in significantly increased epiphytic loads and furthered negative effects of eutrophication (Cook et al., 2011; Östman et al., 2016). However, a study in southern Australia found that when amphipods were absent in temperate seagrass beds, there was no observed difference between algal or epiphyte loads (Poore et al., 2009), though this may have been a result of increased complementary grazing by gastropods inhabiting the same space (Eriksson et al., 2011).

The complex relationships between amphipods and algae extend beyond grazing. In kelp forests, amphipods both eat and live within kelp stipes, significantly decreasing kelp biomass in the process (Conlan and Chess, 1992; Chess, 1993; Gutow et al., 2020). Some amphipod species (e.g., *Ampithoe longimana*; suborder: Senticaudata) live in association

with the algae *Dictyota* spp., using it to avoid predators that find the seaweed unpalatable due to its capacity to produce allelochemicals (Duffy and Hay, 1994). The amphipods themselves are resistant to *Dictyota* chemical defences and are able to graze upon the algae, which in turn promotes higher chemical production and protects the algae further from attacks by other grazers (Hay, 2009). Though larger invertebrates and fish may occasionally take a bite from *Dictyota*, only small herbivores such as amphipods are able to trigger this chemical production within the algae, which is an important mechanism of its survival (Cronin and Hay, 1996).

Further, amphipod grazing on various algae and plants may facilitate a sort of underwater pollination, with grazer mediated spore release documented on reproductive regions of the algae. For example, *Apothysa media* (suborder: Senticaudata) amphipods tear open mature cystocarps on Rhodophyta algae (Buschmann and Santelices, 1987; Buschmann and Bravo, 1990). Rather than directly harming spore development, this grazing method releases mature spores into the water column, some of which stick to the setae of amphipods and are carried even greater

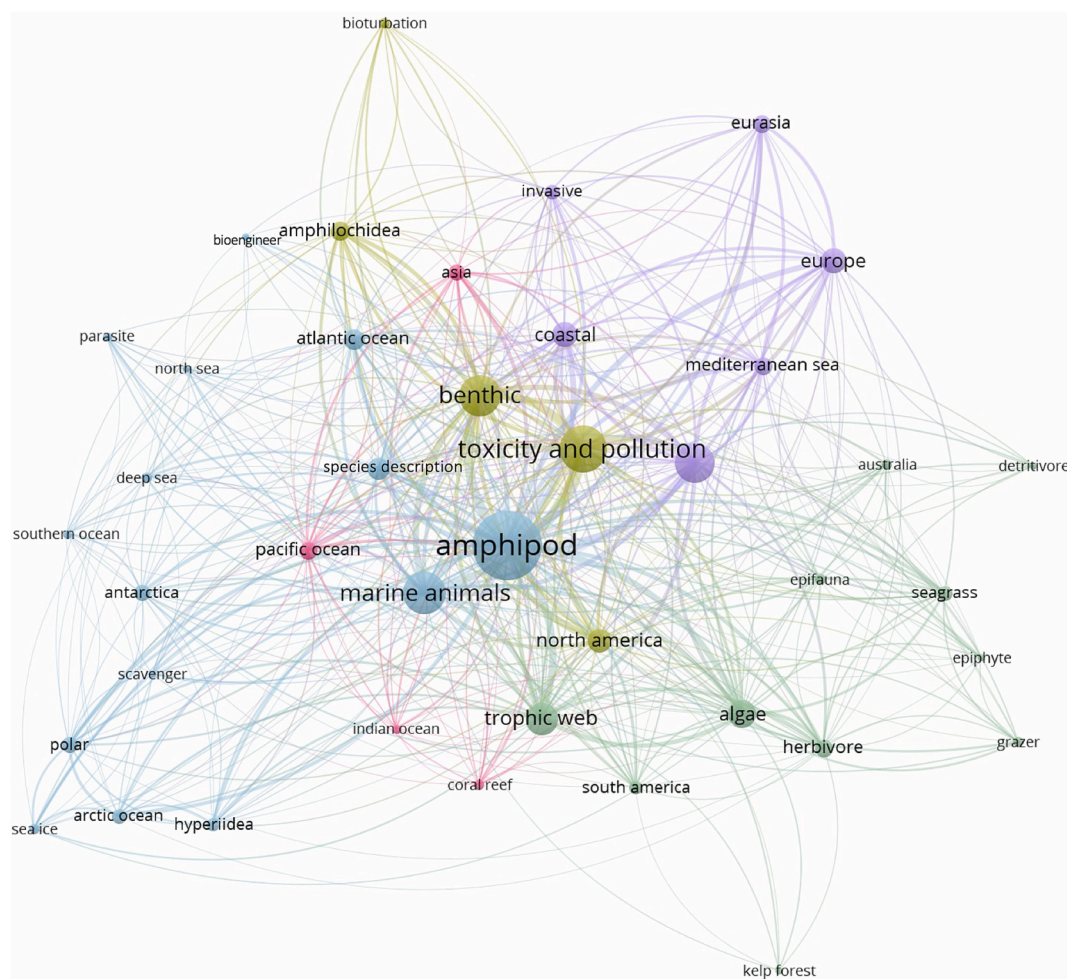


Fig. 4. Clustering of keywords from a Scopus literature search and visualisation in VOSviewer 1.6.19 (Van Eck and Waltman, 2010). The keywords include only those related to habitat and functional role within an ecosystem. Keywords were identified using the string “KEY(marine AND amphipod) AND NOT (KEY(freshwater) AND KEY(estuarine))” with no date restrictions (search performed July 2023). A total of 5103 keywords were identified from 474 peer-reviewed articles after screening for article relevancy. This included keywords from searched titles, abstracts, and author-provided keyword lists. A minimum keyword occurrence threshold of 5 (a requirement met by 304 keywords) was necessary for representation in this network map. The network map clusters keywords by relatedness and occurrence within a theme (indicated by colour), with connected lines representing co-occurrence in papers. Clusters include: Blue – Cold Water Research, Green – Trophic Interactions, Purple – Geographic Species Distribution and Invasives, Gold – Benthic and Toxicity Studies, Pink – Tropical Research. The size of each node represents the number of occurrences across all papers surveyed, and the weight of connecting lines correlates to the number of papers incorporating co-occurrence of the two keywords. For visual clarity and relevance to this work, we manually selected a shorter list of keywords for network analysis based on pertinence to the biological and ecological roles of marine amphipods, then synonymised terms to incorporate broader categories within each node for a final list of 41 keywords (see Sup. Table 1 for more information). Note: there was only one result of the keyword “mangrove,” so this habitat is not represented in the network map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distances (Arrontes, 1999), facilitating the spread and survival possibilities of future generations. In the tropics, amphipod pollination has only been observed once in a study on the tropical seagrass *Thalassia testudinum* in laboratory experiments (Van Tussenbroek et al., 2016), and there are no documented interactions between amphipods and algae in coral reef or mangrove habitats, despite known amphipod presence and association with macroalgal mats in these tropical zones (Winfield et al., 2023). Without knowledge of these relationships, it is difficult to predict the behaviours of tropical amphipods living amidst increased macroalgal growth that is expected with more frequent marine heatwaves of the future (Anton et al., 2020).

3. Anthropogenic impacts affect amphipod communities globally

3.1. Human impacts

There are few places in the ocean left untouched by humans. Plastics litter the deep sea and shallows alike (Chiba et al., 2018), and many studies have documented amphipod ingestion of microplastics throughout the world (Duis and Coors, 2016; Green, 2016; Chae and An, 2017; Bruck and Ford, 2018; Carbery et al., 2018; Campanale et al., 2020; Huang et al., 2021; Botterell et al., 2022), with unclear effects on their health and fitness. Amphipods are heavily impacted by oil spills (Dauvin, 1982; Elmgren et al., 1983; Gomez Gesteira et al., 2003; Ford et al., 2006; Bejarano and Michel, 2016; Demopoulos et al., 2016; Fleeger et al., 2018; Craveiro et al., 2021), waterborne pharmaceuticals (Guler and Ford, 2010; Fong and Ford, 2014; Fabbri and Franzellitti, 2016), and pollutants from wastewater discharge (Swartz et al., 1984; Hall et al., 1998; Woodworth et al., 1999; Carr et al., 2000; Burgos and Rainbow, 2001; Smith and Shackley, 2006; De-La-Ossa-Carretero et al., 2012; De-La-Ossa-Carretero et al., 2016) and mariculture systems (Bouchet and Sauriau, 2008; Wang et al., 2017). Affected individuals have shown embryonic malformations, reproductive failure, and die-offs. The susceptibility of amphipods to damage and their bioaccumulation of heavy metals and toxins has resulted in their frequent use as indicator species for environmental health and pollution levels (e.g., in Gray et al., 1990; Gesteira and Dauvin, 2000; Correia et al., 2002; Ferretti et al., 2002; Fabrega et al., 2012; Parks et al., 2013; Dauvin, 2018). Interestingly, amphipods in the hadal zone have an average lifespan more than four times longer than species dwelling in shallow waters, and hence their relatively slower development is accompanied by potential higher retainment of any toxins consumed or absorbed (Wang et al., 2019). As the basis of many trophic systems across habitats, concerns of plastic and toxin accumulation grow at each subsequent trophic level (Bard, 1999). Many studies on aquatic toxicity use amphipods in the Benthic Opportunistic Polychaete/Amphipod (BOPA) ratio, which has been heralded as a standardised metric to assess the ecosystem quality in coastal waters around the world (Swartz et al., 1982; Conradi et al., 1997; Dauvin and Ruellet, 2007; Maximov and Berezina, 2023), including in the tropics (Mulik et al., 2023).

In intertidal and coastal areas, physical trampling by humans crushes and suffocates many amphipods (Afghan et al., 2020). Boat wake in the shallows forces small invertebrates from the safety of their seagrass perches that are slow to recolonize (Bishop, 2008), and propeller scarring of the benthos causes habitat fragmentation and altered benthic dynamics (Sweatman et al., 2017). Shoreline construction, defence, and building projects also destroy, shift, or degrade coastal habitats (Dethier et al., 2016; Sedano et al., 2020), and fishing (drag or trawl) and dredging activities disturb the substrate homes of amphipods for extended periods (Sánchez-Jerez and Ramos Esplá, 1996; Watling and Norse, 1998; Watling et al., 2001; Casado-Martínez et al., 2007; Mallick et al., 2023).

3.2. Invasive amphipods

Heightened global connectivity and human mobility has increased the geographic spread of many species, especially small biofouling organisms like amphipods (Carlton, 1992; Ros et al., 2013, 2014). For such creatures, avoiding detection in busy ports, ship ballast water, and fouling on recreational boats is common (Carlton, 1992). Predation and competition between alien species and native species are generally considered the most impactful negative consequences of foreign amphipod introduction known to date (Berezina, 2007). However, the impact of alien amphipods likely differs based on several factors including the region invaded, the functional roles of the endemic species, and the flexibility in tolerance of the invasive species. The case of *Caprella mutica* (suborder: Senticaudata) invasions around the world provides compelling examples of this complexity. In temperate coastal waters, *C. mutica* has been observed to rapidly colonise and alter the composition of amphipod communities by outcompeting the natively occurring caprellids (Ashton et al., 2007; Shucksmith et al., 2009). One laboratory-conducted study found that *C. mutica* was capable of displacing native caprellids even with tenfold fewer *C. mutica* than native species present when resources were limited (Shucksmith et al., 2009). In some cases, however, *C. mutica* invasions have increased food sources for local fish in European waters (Katsanevakis et al., 2014) and for seahorses in New Zealand (Ahyong and Wilkens, 2011), allowing population growth of these predators, which in turn keeps the invasive caprellid abundances low. Invasive *Gammarus tigrinus* (suborder: Senticaudata) in the Baltic Sea also have complex implications for locally occurring species (Fig. 2D). *G. tigrinus* outcompete native gammarid amphipods for the most preferred habitats, but despite this, the native species have persisted by moving to neighbouring habitats (Packalén, 2008; Reisalu et al., 2016).

Invasive amphipod success in new regions may be predicted by the species characteristics and tolerance to a range of external conditions, as well as the habitat and regional ecosystem (Berezina, 2007; Cuthbert et al., 2020). Both *C. mutica* and *G. tigrinus* exhibit this flexibility, which likely contributes to their successful establishment around the globe. *C. mutica* have a wide range of environmental tolerances as well as a flexible diet (Cook et al., 2010), and *G. tigrinus* can tolerate hypoxic and warm conditions (Sareyka et al., 2011). While more euryhaline species are likely to be successful invasives, one study suggests that the likelihood of species establishment is based more on the ecological function rather than the biological traits of the species (Devin and Beisel, 2006). Although the distribution and success of several invasive amphipod species have been well documented (e.g., in Ashton, 2007; Ashton et al., 2007; Ashton et al., 2008; Ahyong and Wilkens, 2011; Carlton, 2011), most studies report a lack of understanding of the ecological implications of such invasions in all habitats surveyed.

3.3. Implications of a changing planet for amphipod populations

In addition to the direct effects of human activities on amphipod communities, predicted future climate conditions are expected to challenge these species further. The warming climate will deeply impact amphipods with low temperature tolerances, especially long-lived polar amphipods that depend on substantial patches of sea ice to grow to maturity (Barber et al., 2015). Beyond loss of habitat in the polar regions, ice melt is also expected to release previously frozen particles into the water, increasing the rate of microplastic ingestion in the process (Botterell et al., 2022). Previous impacts of heatwaves on marine communities raise concerns for stability in a warmer future as well. In the 1980s, El Niño conditions took a toll on algae and fish communities alike (Dayton et al., 1998). When fish abundance decreased in Californian kelp forests, the associated decrease in predation allowed amphipods to escape trophic control and subsequently destroy >65% of the kelp through intensified grazing (Dayton et al., 1998). Another future concern with higher temperatures is increased parasitism on amphipods,

particularly by trematode parasites that have the potential to destroy entire amphipod communities in warmer conditions (Mouritsen et al., 2005). Moreover, ocean acidification may not only decrease the condition of invertebrates' physical structures but may also alter the palatability and nutritional content of some common amphipod food sources such as algae (Duarte et al., 2016). The deep seas have maintained largely consistent salinity and temperature conditions to date; however, these habitats face potentially devastating consequences when surface stressors and changes in abiotic conditions eventually reach their depths. For example, one study estimated that >80% of known deep sea biodiversity hotspots around the world will suffer declines in biomass by 2100 (Jones et al., 2014). Overall, the predicted future warming of the oceans, including both increased duration and intensity of marine heatwaves will have serious impacts on amphipod communities with cascading effects on surrounding ecosystems.

More frequent and increased intensity of severe weather events such as tropical storms (hurricanes/cyclones) that are capable of sediment disruption may destroy delicate habitats and assemblages (LaFrance Bartley et al., 2022). Accompanying droughts and rainfall can additionally alter salinity beyond tolerable extremes for many species, and higher rainfall and temperatures would increase polluting outflows and eutrophication in coastal waters especially (Rabalais et al., 2009). Higher levels of eutrophication and more frequent algal blooms have been shown to kill or exclude deposit feeding organisms like amphipods, in addition to altering their community structure (Dorgham, 2014). Studies have also reported that higher pollution in coastal waters may increase amphipod intersexuality as well, which ultimately leads to lowered fitness, declines in amphipod populations, malformation of embryos, and irregular juvenile development via endocrine disruption (Ford et al., 2006, 2007; Sundelin et al., 2008). These combined impacts on amphipod communities will, without urgent research, have unknown downstream effects on ecosystem function.

4. The importance of amphipods in tropical ecosystems

Though amphipods living in temperate and polar regions and the deep sea are somewhat well documented, less is known about those in tropical coastal habitats (coral reefs, mangroves, seagrass beds). For example, our literature search and subsequent clustering analysis showed clear evidence of numerous studies on amphipods in temperate and polar regions, and a comparatively smaller body of literature addressing amphipods in tropic systems (Fig. 4). Clear latitudinal gradients of species richness are established, with higher species diversity in tropical regions (Willig et al., 2003). However, the few studies that exist for the biogeographic diversity of peracarid crustaceans or amphipods specifically tend to show weaker or opposing trends (Burridge et al., 2017; Rivadeneira and Poore, 2020). These trends, or lack thereof, may be confounded by the paucity of data and species descriptions in the lower latitudes. Of note is that from all the papers interrogated in our analysis, there was only one result of the keyword “mangrove” (Fig. 4). Further exploration of amphipod community composition in the tropics is therefore warranted, as knowledge of species occurrence is crucial to defining functional traits and roles within ecosystems (Gross et al., 2022).

Crustacean communities in both temperate and tropical regions thrive in habitats with higher complexity (Kramer et al., 2017). Even coral reefs reduced to mounds of rubble have been shown to host high abundances of amphipods (Fraser et al., 2021). There is ample evidence of amphipod presence in iconic tropical habitats like coral reefs (Thomas, 1993; Hay, 1997), seagrass beds (Mukai and Iijima, 1995) and mangroves (Pan et al., 2021). Amphipods in lower latitudes tend to be physically smaller (Virnstein et al., 1984; Chapelle and Peck, 1999), which can make sampling and observational studies challenging. However, some studies on amphipod and marine plant interactions in the tropics indicate that many relationships may be similar to those documented in temperate zones. For example, amphipod grazers in

Fijian waters consume seagrass leaves and epiphytes (Mukai and Iijima, 1995), while also preserving some seagrass blades to use as nests. Consumption of *Dictyota* and similar red algae by amphipods in the tropics occurs steadily despite the chemical defences produced by the macroalgae (Hay et al., 1988; Paul et al., 1988). Algal grazing occurs in mangrove forests as well, and amphipod shredding of mangrove leaves provides food for other benthic or crypto-benthic organisms (Camilleri, 1992). Only select amphipod species' grazing behaviours have been documented, however, so many behaviours and comparisons to more temperate amphipods are likely missing in the literature.

Despite the high abundance of amphipods in tropical habitats, studies on the utility of amphipods as an indicator of ecosystem health beyond toxicity testing are scarce. Much import is attributed to herbivorous coral reef fish that maintain the algae-coral balance to enhance reef health and productivity (Rasher et al., 2013; Adam et al., 2015), yet the implications of amphipod grazing behaviours on reefs remain mostly unassessed. The few studies on reef amphipods that do exist (e.g., Cruz-Rivera and Paul, 2006) tend to discuss dietary preferences, but there is little information about their higher-level roles in the habitat. There is some indication of amphipod influence on algal dominance in a coral reef microcosm (Brawley and Adey, 1981), but in situ studies on such small organisms present a challenging environment for data collection.

Like their temperate relatives, tropical amphipods will face increased challenges as ocean conditions decline. Delicate nearshore tropical ecosystems are already facing severe impacts as a result of marine heatwaves (Hughes et al., 2018; Duke et al., 2021), though we have little knowledge of the direct and indirect effects on these habitats' amphipod populations. Effects of acidification will also be seen more rapidly in warmer regions, affecting crustacean development and shell durability (Przeslawski et al., 2008). The possibility of faunal shifts must also be considered, even for amphipods with assumed better tolerance to warm conditions. For example, amphipod assemblages in Mexico changed dramatically around the time of El Niño periods in the late 1990s (Ambriz-Arreola et al., 2018). In general, amphipod presence in a habitat largely depends on the structure of the substrate (Kramer et al., 2017; Fraser et al., 2020), so further declines in seagrasses, mangroves, and coral will almost certainly correspond with shifts and declines in amphipod abundance, in turn decreasing food availability for many organisms. Diverse amphipods may be driven to extinction by climate change before they can even be described as species, let alone their functionality and roles in underpinning ecosystem resilience be understood.

5. Conclusions

Amphipods serve as links between trophic levels, bioturbators and benthic-pelagic coupling facilitators, epiphyte controllers, and algal grazers (Figs. 3 & 4). Their presence may determine the faunal, floral, and physical structure of the areas in which they reside, yet data on tropical amphipods is notably lacking in the literature. Therefore, including small invertebrate monitoring surveys in pre-existing tropical surveys would help to establish a baseline understanding of amphipod presence in these habitats. Further research on individual species from various microhabitats within study sites (e.g., free-swimming, site attached or tube building, and meio- or infaunal amphipods) would provide a description of functional niches of each species and potential links between habitats. When combined with “omics”-based approaches, a more detailed understanding of species across latitudes would deepen the current knowledge of evolutionary history of these organisms. Expanding studies to include a wider variety of amphipod species would also reveal the true breadth of functional diversity and the value they provide to various ecosystems to better align with the incredibly high and largely undescribed amphipod species diversity in oceans around the globe. Better tracking and study of tropical invasive species is also warranted as studies have only documented the geographic range of invasive amphipods but not their impacts on the invaded systems.

Tropical ecosystems are at a tipping point, with predicted future declines of these habitats impacting species diversity and abundance of countless invertebrates. There is much work remaining to catalogue and investigate the vast richness, varying roles, and necessity of amphipods in critical tropical marine ecosystems.

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Carmen J. Ritter: Conceptualization, Investigation, Visualization, Writing – original draft, Writing – review & editing. **David G. Bourne:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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