Trends in
Ecology & Evolution

CellPress

Opinion

Sex-specific variation in species interactions matters in ecological communities

Elena Gissi 1,2,3,8,*,@, Maurice Codespoti Goodman[1], Robin Elahi[1,9], Jamie M. McDevitt-Irwin[1,4,10,@], Natalie S. Arnoldi[1], Nur Arafeh-Dalmau[1,5,6,@], Christopher J. Knight[1,@], Carolina Olguín-Jacobson[1,@], Melissa Palmisciano[1], Ceyenna M. Tillman[1], Giulio A. De Leo[1,11,@], and Fiorenza Micheli[1,7,12,@]

Understanding how natural communities and ecosystems are structured and respond to anthropogenic pressures in a rapidly changing world is key to successful management and conservation. A fundamental but often overlooked biological characteristic of organisms is sex. Sex-based responses are often considered when conducting studies at organismal and population levels, but are rarely investigated in community ecology. Focusing on kelp forests as a model system, and through a review of other marine and terrestrial ecosystems, we found evidence of widespread sex-based variation in species interactions. Sex-based variation in species interactions is expected to affect ecosystem structure and functioning via multiple trophic and nontrophic pathways. Understanding the drivers and consequences of sex-based variation in species interactions can inform more effective management and restoration.

Biological sex is rarely considered in community ecology

In recent years, **community** (see Glossary) ecology has undergone a paradigm shift, moving beyond species as the sole operational unit around which **species interactions** and **food web** dynamics are structured, towards a trait-based lens. By both broadening to the level of functional groups [1] and narrowing to consider **intraspecific variation** [2], these approaches have improved predictions of ecosystem dynamics [3,4], ecological responses to environmental change [2,5], and ecological resilience [6,7]. However, the role of **biological sex** as a fundamental characteristic of living organisms has been overlooked in community ecology [8].

Biological sex affects the physiology, metabolism, and behaviour of organisms across taxa and ecosystems [9]. Most (90–94%) studies at the organismal, population, and species levels that considered sex have noted differences in biological responses among sexes through laboratory and field experiments [8,10,11]. Yet, few empirical studies have evaluated the role of biological sex in the dynamics and functioning of whole ecological communities [8,12]. Community-wide, sex-related effects are likely to occur, as sex is known to influence energetic requirements [13], foraging behaviour [14], body size [15], spatial distribution and population dynamics [16], home ranges [17], and phenology [18] in a wide range of marine and terrestrial species. Recent theoretical models in community ecology have highlighted that sex-based differences in consumers can have important consequences for consumer-resource coexistence, abundance, and dynamics [12,18], and that these differences can affect food web persistence and structure [19].

The interplay between ecology and evolution is also important. For example, traits that have evolved via sexual selection can have direct and indirect effects on species interactions and

Highlights

Biological sex affects the morphology, physiology, behaviour, and distribution of organisms and populations.

Integrating intraspecific variation of biological traits into community dynamics has improved our understanding of food web and ecosystem dynamics and stability. However, biological sex is rarely considered.

The inclusion of sex-specific variation in theoretical models has highlighted that sex-based differences can significantly influence community dynamics, but empirical tests are limited.

Methodological and logistical challenges often prevent the consideration of organisms' sex in the field, limiting our understanding of the role of sex in community functioning. Where these limitations have been overcome, field studies highlighted sex-based species interactions and their cascading ecological outcomes in marine, freshwater, and terrestrial ecosystems.

[1]Oceans Department, Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA
[2]National Research Council, Institute of Marine Science, Venice, 30122, Italy
[3]National Biodiversity Future Center, Palermo, 90133, Italy
[4]Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93117, USA
[5]Department of Geography, University of California Los Angeles, Los Angeles, CA 90095, USA
[6]Centre for Biodiversity and Conservation Science, School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

https://doi.org/10.1016/j.tree.2024.07.006

community processes, such as morphological, physiological, and behavioural characteristics, which have been well studied in vertebrates across a range of ecosystems [20]. In addition, variation in sex ratios is key to evolving sex differences in reproductive behaviour, including mate competition, mate choice, and parental care [16]. In wild populations, skewed sex ratios are often observed, with female-biased populations in seagrasses [21], copepods [22], and mammals [23], and male-biased in *Schistosoma* parasites [24], insects [25], birds [24,26], and dioecious angiosperms [27]. Moreover, sex ratios can vary in time and space [16,28,29], as in the case of the mosquitofish (*Gambusia affinis*) [30], snowy plovers (*Charadrius nivosus*) [31], and the European eel (*Anguilla anguilla*) [32]. Male–female intraspecific demographic variation in predators can influence consumption rates and prey densities [30,33]. Yet, the role of sex-based differences in altering species interactions and the resulting **community structure** and **community dynamics** remains a major knowledge gap in ecology.

Here, we explore how sex-based differences in species interactions may affect community dynamics. We draw on examples from kelp forest ecosystems, where previous studies have demonstrated the strong influence of cascading **trophic** and **nontrophic interactions** on community structure and dynamics, and on **community persistence**. We also included examples from other terrestrial and marine ecosystems to begin exploring the generality of sex-based variation in species interactions across communities and ecosystems.

Sex-specific variation in species interactions in kelp forest ecosystems

Kelp forests are iconic temperate ecosystems with important ecological, economic, and cultural value [34,35]. Studies of kelp forests have contributed to the development of general ecological concepts and theory, including the role of foundation species [36,37], **cascading interactions** [34,38,39], top-down and **bottom-up effects** in food web regulation [40], alternative stable states [41], and climate-related regime shifts [42–44]. In particular, the globally distributed giant kelp (*Macrocystis pyrifera*) has been studied since the 1960s (reviewed in [45]).

Pioneering work on giant kelp forests in Alaska, USA, demonstrated a linear chain of trophic effects (Figure 1A), where a reduction in the abundance of kelps was related to increased predation by killer whales (*Orcinus orca*) on sea otters (*Enhydra lutris*), sea otters being keystone predators that suppress outbreaks of sea urchin grazing and thus prevent deforestation [34,46]. Over time, this textbook example of a trophic cascade expanded to reflect other species interactions (Figure 1B) and the role of bottom-up processes [45]. In addition to sea otters, other predators, such as sheepheads (*Semicossyphus pulcher*), spiny lobsters (*Panulirus interruptus*), and sunflower sea stars (*Pycnopodia helianthoides*), also influence sea urchin densities and behaviours [47–49], while microcarnivorous fishes can indirectly benefit kelp forests by consuming amphipod mesograzers [39]. Beyond trophic interactions, temperature, nutrients, storms, and other abiotic features influence the population dynamics of giant kelp and the downstream consequences for the associated community [43,50,51].

Using biological sex as a lens through which we re-examine food web dynamics (Table S1 in the supplemental information online), we found widespread evidence of sex-based variation in species interactions between two or more species or functional groups in kelp forests (Figure 1C). We categorised examples of top-down and bottom-up interactions into typologies (Figure 2, Table S2 in the supplemental information online).

Predators

Functional redundancy in predators is hypothesised to allow kelp forests to persist and prevent transitions to a sea-urchin dominated 'barren' state [52]. In Northeast Pacific kelp ecosystems,

[7] Stanford Center for Ocean Solutions, Stanford University, Pacific Grove, CA 93950, USA
[8] https://www.ismar.cnr.it
[9] https://elahi.github.io/
[10] https://jamiemcdevittirwin.github.io
[11] https://deleolab.stanford.edu/
[12] https://michelilab.stanford.edu/

*Correspondence:
elena.gissi@cnr.it (E. Gissi).
@X: @GissiElena, @CnrIsmar (E. Gissi), @AdalmauNur (N. Arafeh-Dalmau), @jamiemcirwin (J.M. McDevitt-Irwin), @JellyfishVibes (C. Olguín-Jacobson), @CKnight_MarSci (C.J. Knight), @FiorenzaMicheli, @MicheliLab (F. Micheli), and @giuliodeleo (G.A. De Leo).

the main predators of sea urchins include sea otters, sheepheads, spiny lobsters, and sunflower sea stars. Sea otters can have different foraging strategies depending on their sex and age; and these affect population structure and kelp forest community dynamics. For example, male otters more often target sea urchins and have more generalist diets than females. However, younger males predominantly eat large urchins and clams and tend to have more specialised diets than adults [53–55]. These dietary differences are partly driven by differences in mobility and home range. Females are more reliant on the kelp canopy for a nursery habitat and spend more time at the surface with pups (i.e., prioritising parental care [55,56]), which results in smaller home ranges and restricted mobility relative to males [53,55]. However, while larger home ranges and high mobility might increase resilience to some stressors, these characteristics also make male sea otters more susceptible to mistargeted predation by white sharks (*Carcharodon carcharias*) [17]. This example illustrates how myriad sex-based interactions influence sea otter distribution, prey preferences, and age/population structure, which can directly impact predation rates and, potentially, the otters' role in controlling sea urchin populations.

Sea otters are not the only kelp forest mesopredators for which trophic interactions differ between the sexes. South of Point Conception, California, USA, sheepheads, spiny lobster, and sunflower sea stars serve a similar ecological role as predators of urchins and other invertebrates. Sheepheads are sequential protogynous hermaphrodites, where they are born as females and change into males. They display clear morphological differences in colour and size, with males being larger than females, and differences in diel movement and site fidelity [57]. Males and females also have different diets, with larger individuals, typically males, consuming more sea urchins than smaller females [58,59]. These differences have important implications for management and conservation. For instance, failure to consider sheephead sex ratios can bias stock assessments [60]. Importantly, recreational and commercial fishing of sheepheads is typically size-selective, such that males are more susceptible to fishing pressure. Size-selective fishing truncates sheephead size distribution and skews sex ratios, reducing predatory control on sea urchin populations in kelp forests [52,59]. In contrast to sheepheads, little is known about sex-specific diet and foraging behaviour in spiny lobsters and sunflower sea stars, and their potential consequences at the community level. Thus, sex-based interactions between predators and prey may be common in kelp forests.

In other ecosystems, sex-based interactions among predators and prey are also common and may influence overall trophic interactions and population dynamics. Examples of sex-selective predation are known in freshwater systems for brook trout (*Salvelinus fontinalis*) on calanoid copepod populations [61], in terrestrial systems for Northern goshawks (*Accipiter gentilis*) on tawny owls (*Strix aluco*) [62], and for various carnivores on ungulates [63]. Sex-selective predation can have a stabilising or destabilising effect on prey populations, depending on predator bias and the prey's mating system [64,65]. These examples underscore the influence of sex-specific predation on predator–prey dynamics. The diverse effects of sex-specific predation uniquely modulate interactions within various ecosystems and cannot be inferred solely from predation rates and species abundance.

Herbivores

Further down the food web, herbivores can have sex-specific impacts on kelps. Sex-specific behaviour of herbivores can affect the biomass and abundance of algae, with likely implications for algae persistence. For example, female amphipods (*Pseudopleonexes lessoniae*) build nests on the blades of giant kelp, reducing blade length and surface by 40% and 55%, respectively [66], possibly influencing kelp forest productivity and biomass.

Glossary

Biological sex: characteristics of an organism (e.g., male, female, or hermaphrodite) determined by genetics and/or the environment that regulate the production of gametes and can influence the physiology, morphology, and behaviour of individuals.

Bottom-up effects: effects from species at a lower trophic level affecting or controlling the community structure of higher trophic levels by means of resource limitation or availability.

Cascading interactions: indirect interactions that occur if predators reduce the abundance or alter the behaviour of their prey, thereby enhancing survival and releasing the next lowest trophic level from predation (or herbivory, if the intermediate trophic level is a herbivore). Cascading interactions occur across a minimum of three trophic levels and can control entire ecosystems.

Community: assemblage of at least two species that are organised into food webs in which each species interacts directly and indirectly within a defined geographic area.

Community dynamics: the changes in community structure and composition over time and space, following, for instance, cascading interactions, bottom-up effects, or anthropogenic and environmental disturbances.

Community stability: the capacity of an ecological community to return to its equilibrium state after perturbation or to not experience unexpected large changes in its characteristics across time.

Community structure: the number and type of species (composition) and their interactions in a given community, also including species distribution, abundance, demography, and interactions among coexisting populations.

Food web: a network of trophic and nontrophic interactions among species that co-occur within an ecological community.

Intraspecific variation: variation among individuals of the same species (e.g., differences due to biological sex or ontogeny).

Nontrophic interactions: any nonconsumptive interactions between two species; for instance, two or more species that have a net benefit from their interaction, or when the behaviour of a species affects the availability or status of another species.

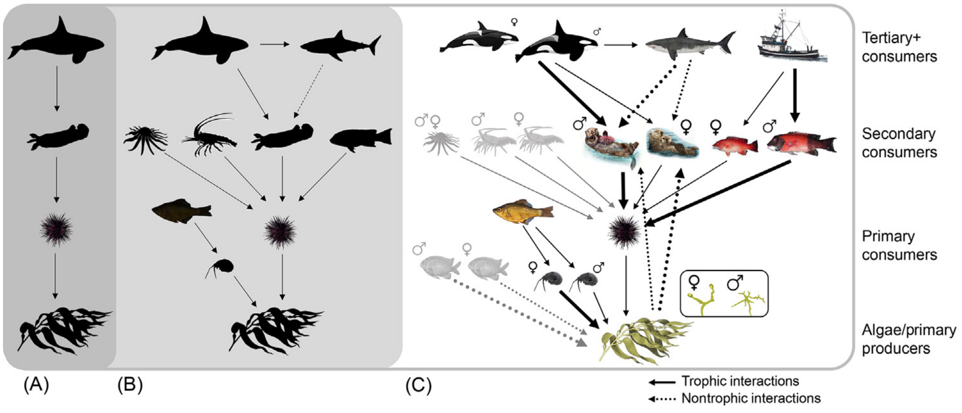
Furthermore, female herring cales (*Odax cyanomelas*) in Australia bite the meristems of the stipitate golden kelp (*Eklonia radiata*) more often than males during the female spawning period, weakening the algae and theoretically increasing the likelihood of kelp clearings following disturbances [67].

Sex-specific behaviour in herbivorous fishes can also impact benthic algae in kelp forests. Garibaldi (*Hypsypops rubicundus*) are conspicuous inhabitants of the kelp forests in southern and Baja California. Like other damselfishes (Pomacentridae), they maintain and defend algal gardens on temperate and tropical reefs; males also create algal 'nests' to attract females for egg deposition. Male garibaldi selectively remove certain algal species from their territories, thereby promoting unique habitats on the reef. The quantity and quality of algal mats is associated with female behaviour and egg-laying, suggesting there is strong sexual selection for this male trait [68,69]. These sexually selected traits, and their ecological consequences, have been studied in other temperate reefs [67,70]. Thus, the amount of male garibaldi on the reef may influence the community composition of benthic algae.

Sex-specific differences in diet were found for analogous species in other ecosystems. For instance, in controlled experiments with Mediterranean sea urchins (*Arbacia lixula* and *Paracentrotus lividus*), females consumed 50% more algae than males to meet the energetic cost of egg production [71], potentially resulting in larger effects on the biomass and recruitment of algae. In a lentic freshwater system, female amphipods of *Gammarus aequicauda* tend to be less selective and have higher consumption and feeding rates than males, yet a male-biased population may lead to less grazing pressure overall [72]. Similarly, in terrestrial systems, the female-biased population of the seed eating fig-wasp (*Chalcidoidea* spp.) restricts the parasitic impacts of sedentary males that solely consume seeds, compared with mobile females that consume seeds and pollinate hosts [73,74]. Sexual dimorphism also influences the dietary habits of birds,

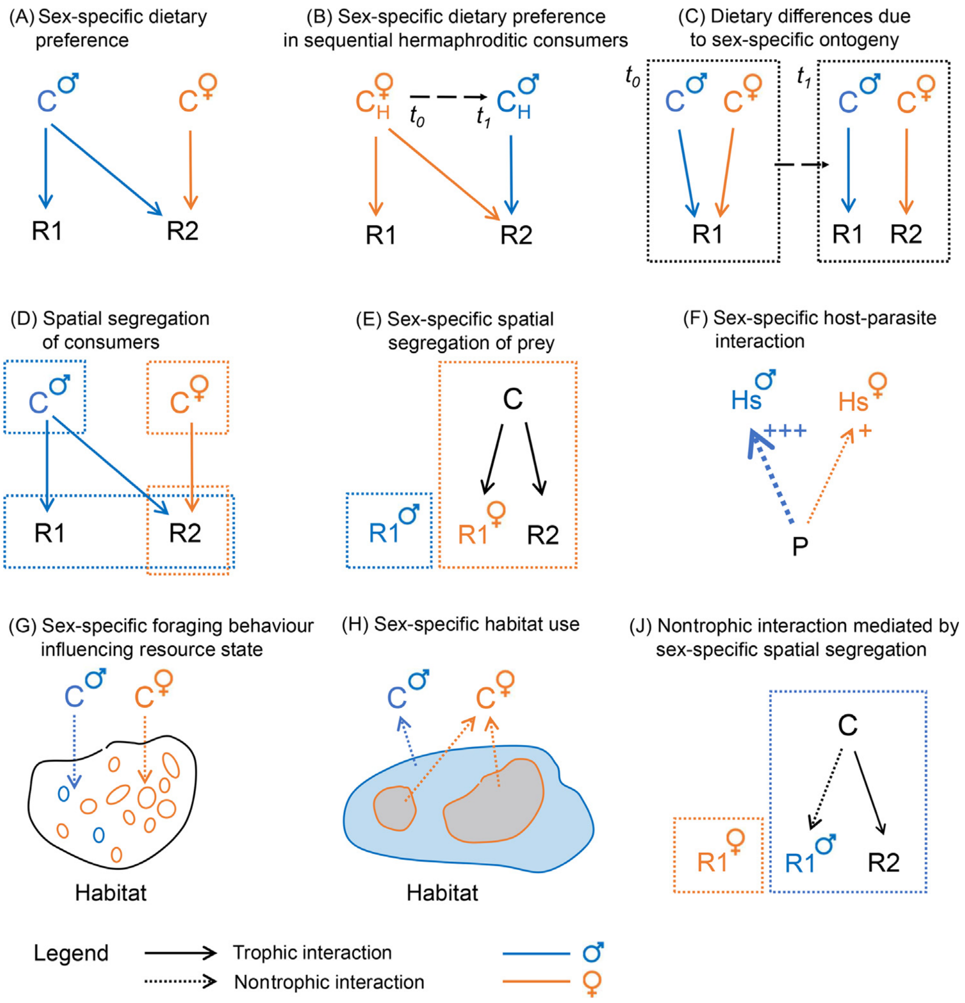
Species interactions: the assemblage of populations of at least two different species that interact directly and indirectly within a defined geographic area.

Trophic interactions: any consumptive interaction between two species that implies a transfer of energy from the bodies of individuals of one species to those of a different species, (e.g., predation between a predator and a prey, herbivory between a consumer and a resource, and parasitism between a host and a parasite).



Trends in Ecology & Evolution

Figure 1. Food web models emerging from empirical evidence of trophic and nontrophic interactions in kelp food webs. (A) A model of Northeast Pacific kelp forest ecosystems as a linear chain of trophic effects, where a reduction in kelp's abundance was attributed to increased predation by killer whales (*Orcinus orca*) on sea otters (*Enhydra lutris*), a keystone predator that suppresses grazing outbreaks by urchin (*Strongylocentrotus purpuratus*) and thus deforestation [34,46]. (B) Evolution of the model, updating the trophic cascade to reflect other species interactions and the role of bottom-up processes as documented, for instance, by [45]. (C) Emerging model with sex-specific variations in species interactions represented through existing empirical research for a composite food web of kelps in temperate regions. Black unbroken arrows represent trophic interactions, black broken arrows represent nontrophic interactions, and grey arrows represent known trophic interactions for which there is no evidence about sex-specific influences; thickness represents the intensity of effects by or on males and females.



Trends in Ecology & Evolution

Figure 2. Types of sex-based species interactions emerging from studies on kelp forests. Each panel represents a type of interaction: sex-specific dietary preferences in sea otters (*Enhydra lutris*) (A) and in sheephead (*Semicossyphus pulcher*) (B); dietary differences due to sex-specific ontogeny in wrasse (*Notolabrus fucicola*) (C); spatial segregation of consumers in tanner crabs (*Chionoecetes tanneri*) (D), and of prey in redspotted catshark (*Schroederichthys chilensis*) (E); sex-specific host–parasite interactions between *Sarcocystis neurona* (causing protozoal encephalitis) and sea otters (F); sex-specific foraging behaviour in herbivorous fish (damselfish, *Parma victoriae*) influencing resource state (G); sex-specific habitat use in sea otters (H); and nontrophic interactions mediated by sex-specific spatial segregation between great white sharks (*Carcharodon carcharias*) and sea otters (J). These types of interaction are not mutually exclusive but are combined across the food web. Examples from kelp forests are presented in Table S2 in the supplemental information online. Abbreviations: C, consumers; F, females; H, hermaphrodites; Hs, host; M, males; P, parasites; R, resource. Unbroken arrows represent trophic interactions, broken arrows represent nontrophic interactions, and blue and orange colours are used for sex-specific variation in species interactions.

such as the great bustard (*Otis tarda*), where males consume more weeds while females more fruits and seeds [75]. These dietary differences, along with their spatial segregation outside the mating season, suggest that males and females apply different levels of grazing pressure to plant species and also provide variation in seed distribution. Collectively, these examples provide initial evidence, generate hypotheses, and raise new research questions for how sex-specific differences in the herbivore guild can impact ecosystem productivity and biomass, overall guild composition, and stability to disturbances.

Primary producers and bottom-up influences

Kelp is a foundation species that forms a physical habitat supporting complex food webs [76]. Protection and restoration initiatives have intensified globally to reverse declines in kelp forests [77]. Sex-specific recruitment and persistence of kelps may influence kelp recovery and effective restoration. Sex determination in kelps (i.e., the development of gametophytes into males or females) is species-specific and depends on the interaction of genetics with environmental factors (e.g., temperature, salinity) influencing the postgermination mortality of either males or females [78,79]. Thus, high temperatures induced by climate change could modulate the ratios of female to male kelp gametophytes, hypothetically altering egg fertilisation rates [80]. Skewed sex ratios in warming oceans could hinder kelp fertilisation and sporophyte production, since the abundance and fertility of females determines the overall recruitment of kelp sporophytes [81]. Understanding the possible drivers of kelp sex ratios, sexual variation, and sporophyte production across latitudes and environmental conditions [80] is essential to predicting the persistence of kelp forests and informing their protection and restoration.

The fate of kelp populations will reverberate throughout the food web through bottom-up influences intersecting with top-down cascading effects. The observed global decline in kelp forests driven by local anthropogenic activities, climate change, and destructive grazing [44,82,83] could have sex-specific bottom-up influences on consumers. For instance, the loss of the kelp habitat can influence the population dynamics of sea otters by influencing the survival of females and pups, which rely on kelp for their nursing habitat [53,55], as well as other species that rely on kelp as food and refuge, particularly during reproduction and juvenile recruitment.

Sex determination, recruitment, and the persistence of primary producers is expected to have complex influences on ecosystem structure and functioning via multiple trophic pathways. For example, sex-based differences in energy allocation and defensive chemical production in terrestrial plants can control the abundance of herbivores and their predators [84,85]. The omnivorous common flower bug (*Anthocoris nemorum*) develops faster on male plants of its dioecious host of grey willow (*Salix cinera*), so, its prey, the blue willow beetle (*Pharatora vulgatissimia*), shows a behavioural preference for the female plant. However, *A. nemorum* follows its prey to female plants, leading to plant-sex-biased predation [86]. An expanded understanding of the drivers and consequences of species interactions, including sex-based differences among primary producers, can help managers in reversing ecosystem degradation.

Concluding remarks

Understanding the processes that drive the structure and function of ecological communities is a fundamental goal of ecology and has implications for conservation, management, and restoration. Studies on kelp forests show that sex-specific variation in species interactions exists at multiple trophic levels. Thus, the available empirical evidence generates a more complex and nuanced model for community dynamics, compared with the textbook trophic cascade, and raises new questions about the community-wide consequences of sex-based variation in species interactions for ecosystem structure, function and resilience. We propose that the inclusion of sex-based differences in empirical and theoretical community ecology research will improve our understanding of community dynamics and persistence, and is likely to prove valuable in many food webs and ecosystems. Ecological studies are often missing a fundamental characteristic by omitting biological sex, which may be as important as (and is often confounded with) body size, which is, in contrast, broadly considered in ecological research. Ecologists should consider explicitly incorporating interaction strengths among males, females, and hermaphrodites, whenever possible, since sex is as important a source

Outstanding questions

How do sexual phenotypes (e.g., size, behaviour) that manifest across the life cycle and ontogeny influence sex-specific variation in species interactions? Does biological sex influence the strength of interactions across the trophic levels of food webs?

Does sex-specific variation influence other types of species interactions such as mutualism, commensalism, and parasitism?

Spatial and temporal variation in sexual segregation and in sex ratios may significantly impact predator–prey dynamics. Additionally, sex-based resource segregation can influence bottom-up control mechanisms within food webs. How do sex-based spatial and temporal patterns collectively affect an ecosystem's processes and stability?

How do sex-based intraspecific differences and the strength of interspecific interactions influence community's stability in response to global climate change and other local anthropogenic pressures?

What new approaches and techniques can enable studies of sex-specific variation in species interactions in field research, such as in species that are not sexually dimorphic and for which sex-specific differences are not visually apparent, or where one sex is less accessible than the other?

of individual variation in communities [87,88] as ontogeny or genotype [89]. Moreover, in cases where sex-based variation in traits (e.g., body size, aggression) are under strong sexual selection and have associated ecological consequences (e.g., trophic niche breadth, density-dependence), there is potential for ecoevolutionary dynamics [20].

The typologies of sex-based interactions we detected by examining kelp forests as a model system (Figure 2) can inform empirical and modelling studies, and can be expanded by considering sex-based species interactions in other ecosystems. Other typologies can be detected by considering the specificities of marine, terrestrial, and freshwater systems, or other types of species interactions (e.g., mutualism, commensalism, and parasitism). For instance, sex-based differences in the foraging patterns of male and female pollinators, such as unequal visit costs or the quality and quantity of transfers, affect plant reproduction and may influence the movement of pollen at the community level, and **community stability** [74]. The extent to which the typologies in simple food webs (Figure 2) will scale up to predict patterns at the community level remains to be determined and is a conspicuous knowledge gap. Where ecologists have incorporated sex into simple (two or three species) theoretical food webs, they have found that sex-based differences can significantly alter community dynamics [12,19]. For example, sexual dimorphism in consumers' attack rates can alter the potential for consumer-resource coexistence in a two-species model with male and female predators [12]. Moreover, the amount of trophic inflow into males with less parental investment plays an important role in system persistence and structure in a three-species food web model [19].

Expanding the understanding of sex-specific differences in species interactions and their role in community dynamics will be essential in the context of climate change, as males, females, and hermaphrodites can respond differently to climatic stressors [11,90]. Most studies examined herein were field-based, but these studies were skewed towards species with easily distinguishable sexes (e.g., by sexual dimorphism). Laboratory experiments commonly apply an *a priori* classification of groups by sex without clear justification or hypotheses for this grouping [91]. As laboratory-based studies may not approximate interspecific interaction rates at ecologically relevant scales [92], it is important to evaluate the ecological effects of sex-specific variation in species interactions in the field. Characterising and reporting sex-based differences through a set of traits that contribute to the overall sex phenotype [93] will help uncover whether and how any sex-specific variation matters and what drives it. However, there are major methodological and logistical challenges in accounting for sex in ecological research, particularly in the field (reviewed in [8]).

Future research may address new approaches and techniques for evaluating sex-specific variation in species interactions in field research (see Outstanding questions). For example, to explore the role of sex in explaining the variation in predation, researchers can implement 'natural experiments' by conducting the same field experiment at sites with different sex ratios of the consumers or the resources, or in areas where females and males are known to segregate. The setting of the techniques and related metrics in future studies will be driven by the research objectives and the hypothesis, which are contextual and species-specific [91,94].

Empirical research which illuminates the role of biological sex within ecological communities has the potential to reshape our approach to biodiversity conservation ([8] and references therein). Systematically considering sex-specific variation in community ecology will foster new discoveries, promote methodological innovation, and help answer open questions about community dynamics in a rapidly changing world.

Author contributions

E.G., M.C.G., J.M.I., R.E., N.S.A., and F.M. designed the study and wrote the first draft of the manuscript, with the coordination of E.G.; all authors (E.G., M.C.G., J.M.I., R.E., N.S.A., N.A.-D., C.J.K., C.O.-J., M.P., C.M.T., G.A.D.L., and F.M.) performed the search for case studies of sex-specific variation in species interactions and contributed to the final version of the article; E.G. designed and prepared the figures.

Acknowledgments

Funding was provided to E.G. by the EU Horizon 2020 research and innovation program under the Marie Skłodowska-Curie Actions, Individual Fellowship (grant agreement #893614). F.M. and G.A.D.L. also acknowledge support from the US National Science Foundation (2108566). This study reflects only the views of the authors. The Research Executive Agency and the European Commission are not responsible for any use that may be made of the information it contains.

Declaration of interests

The authors have no interests to declare.

Supplementary information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2024.07.006.

References

1. Mammola, S. *et al.* (2021) Concepts and applications in functional diversity. *Funct. Ecol.* 35, 1869–1885
2. Gårdmark, A. and Huss, M. (2020) Individual variation and interactions explain food web responses to global warming. *Philos. Trans. R. Soc. B Biol. Sci.* 375, 20190449
3. Green, S.J. *et al.* (2022) Trait-based approaches to global change ecology: moving from description to prediction. *Proc. R. Soc. B Biol. Sci.* 289, 20220071
4. Marjakangas, E-L. *et al.* (2022) Trait-based inference of ecological network assembly: a conceptual framework and methodological toolbox. *Ecol. Monogr.* 92, e1502
5. Nielsen, E.S. *et al.* (2021) Distinct interspecific and intraspecific vulnerability of coastal species to global change. *Glob. Change Biol.* 27, 3415–3431
6. De Battisti, D. (2021) The resilience of coastal ecosystems: a functional trait-based perspective. *J. Ecol.* 109, 3133–3146
7. Turner, M.G. and Seidl, R. (2023) Novel disturbance regimes and ecological responses. *Annu. Rev. Ecol. Evol. Syst.* 54, 63–83
8. Gissi, E. *et al.* (2023) Sex analysis in marine biological systems: insights and opportunities. *Front. Ecol. Environ.* 21, 324–332
9. Tannenbaum, C. *et al.* (2019) Sex and gender analysis improves science and engineering. *Nature* 575, 137–146
10. Ellis, R.P. *et al.* (2017) Does sex really matter? Explaining intraspecies variation in ocean acidification responses. *Biol. Lett.* 13, 20160761
11. Pottier, P. *et al.* (2021) Sexual (in)equality? A meta-analysis of sex differences in thermal acclimation capacity across ectotherms. *Funct. Ecol.* 35, 2663–2678
12. De Lisle, S.P. *et al.* (2022) Complex community-wide consequences of consumer sexual dimorphism. *J. Anim. Ecol.* 91, 958–969
13. Donelan, S.C. and Trussell, G.C. (2020) Sex-specific differences in the response of prey to predation risk. *Funct. Ecol.* 34, 1235–1243
14. Bennison, A. *et al.* (2022) A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *R. Soc. Open Sci.* 9, 210520
15. Moranta, J. *et al.* (2020) The effects of fishing on the ontogeny of trophic position and body condition of a small-sized temperate marine fish. *Mar. Environ. Res.* 161, 105055
16. Kappeler, P.M. *et al.* (2023) Sex roles and sex ratios in animals. *Biol. Rev.* 98, 462–480
17. Moxley, J.H. *et al.* (2019) Non-trophic impacts from white sharks complicate population recovery for sea otters. *Ecol. Evol.* 9, 6378–6388
18. Nakazawa, T. *et al.* (2023) Why sex matters in phenological research. *Oikos* 2023, e09808
19. Kawatsu, K. (2018) Ecological effects of sex differ with trophic positions in a simple food web. *Ecol. Evol.* 8, 1239–1246
20. Giery, S.T. and Layman, C.A. (2019) Ecological consequences of sexually selected traits: an eco-evolutionary perspective. *Q. Rev. Biol.* 94, 29–74
21. Shelton, A.O. (2010) The origin of female-biased sex ratios in intertidal seagrasses (*Phyllospadix* spp.). *Ecology* 91, 1380–1390
22. Hirst, A.G. *et al.* (2010) Does predation controls adult sex ratios and longevities in marine pelagic copepods? *Limnol. Oceanogr.* 55, 2193–2206
23. Clutton-Brock, T.H. and Iason, G.R. (1986) Sex ratio variation in mammals. *Q. Rev. Biol.* 61, 339–374
24. Székely, T. *et al.* (2014) Adult sex ratio variation: implications for breeding system evolution. *J. Evol. Biol.* 27, 1500–1512
25. Teder, T. and Kaasik, A. (2023) Early-life food stress hits females harder than males in insects: a meta-analysis of sex differences in environmental sensitivity. *Ecol. Lett.* 26, 1419–1431
26. Donald, P.F. (2007) Adult sex ratios in wild bird populations. *Ibis* 149, 671–692
27. Munné-Bosch, S. (2015) Sex ratios in dioecious plants in the framework of global change. *Environ. Exp. Bot.* 109, 99–102
28. Schacht, R. *et al.* (2022) Adult sex ratios: causes of variation and implications for animal and human societies. *Commun. Biol.* 5, 1–16
29. Melià, P. *et al.* (2006) Sex differentiation of the European eel in brackish and freshwater environments: a comparative analysis. *J. Fish Biol.* 69, 1228–1235
30. Fryxell, D.C. *et al.* (2015) Sex ratio variation shapes the ecological effects of a globally introduced freshwater fish. *Proc. R. Soc. B Biol. Sci.* 282, 20151970
31. Eberhart-Phillips, L.J. *et al.* (2017) Sex-specific early survival drives adult sex ratio bias in snowy plovers and impacts mating system and population growth. *Proc. Natl. Acad. Sci. U. S. A.* 114, E5474–E5481
32. Bevacqua, D. *et al.* (2019) A demographic model for the conservation and management of the European eel: an application to a Mediterranean coastal lagoon. *ICES J. Mar. Sci.* 76, 2164–2178
33. Cuthbert, R.N. *et al.* (2020) Examining intraspecific multiple predator effects across shifting predator sex ratios. *Basic Appl. Ecol.* 45, 12–21
34. Estes, J.A. *et al.* (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282, 473–476
35. Eger, A.M. *et al.* (2023) The value of ecosystem services in global marine kelp forests. *Nat. Commun.* 14, 1894
36. Dayton, P.K. (1972) Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In *Proceedings of the Colloquium*

on Conservation Problems in Antarctica (Parker, B.C., ed.), pp. 81–96, Allen Press

37. Lamy, T. *et al.* (2020) Foundation species promote community stability by increasing diversity in a giant kelp forest. *Ecology* 101, e02987
38. Arkema, K.K. *et al.* (2009) Direct and indirect effects of giant kelp determine benthic community structure and dynamics. *Ecology* 90, 3126–3137
39. Davenport, A.C. and Anderson, T.W. (2007) Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. *Ecology* 88, 1548–1561
40. Dayton, P.K. *et al.* (1999) Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol. Monogr.* 69, 219–250
41. Filbee-Dexter, K. and Scheibling, R. (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar. Ecol. Prog. Ser.* 495, 1–25
42. McPherson, M.L. *et al.* (2021) Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. *Commun. Biol.* 4, 1–9
43. Tegner, M.J. and Dayton, P.K. (1987) El Niño effects on southern California kelp forest communities. In *Advances in Ecological Research* (Vol. 17) (Macfadyen, A. and Ford, E.D., eds), pp. 243–279, Academic Press
44. Wernberg, T. *et al.* (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353, 169–172
45. Schiel, D.R. and Foster, M.S. (2015) *The Biology and Ecology of Giant Kelp Forests* (1st edn), University of California Press
46. Estes, J.A. and Palmisano, J.F. (1974) Sea otters: their role in structuring nearshore communities. *Science* 185, 1058–1060
47. Cowen, R.K. (1983) The effects of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* 58, 249–255
48. Tegner, M.J. and Levin, L.A. (1983) Spiny lobsters and sea urchins: analysis of a predator–prey interaction. *J. Exp. Mar. Biol. Ecol.* 73, 125–150
49. Galloway, A.W.E. *et al.* (2023) Sunflower sea star predation on urchins can facilitate kelp forest recovery. *Proc. R. Soc. B Biol. Sci.* 290, 20221897
50. Byrnes, J.E. *et al.* (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. *Glob. Change Biol.* 17, 2513–2524
51. Foster, M.S. and Schiel, D.R. (2010) Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. *J. Exp. Mar. Biol. Ecol.* 393, 59–70
52. Eisaguirre, J.H. *et al.* (2020) Trophic redundancy and predator size class structure drive differences in kelp forest ecosystem dynamics. *Ecology* 101, e02993
53. Elliott Smith, E.A. *et al.* (2015) The cost of reproduction: differential resource specialization in female and male California sea otters. *Oecologia* 178, 17–29
54. Rechsteiner, E.U. *et al.* (2019) Sex and occupation time influence niche space of a recovering keystone predator. *Ecol. Evol.* 9, 3321–3334
55. Thometz, N.M. *et al.* (2016) Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behav. Ecol.* 27, 1552–1566
56. Nicholson, T.E. *et al.* (2018) Gaps in kelp cover may threaten the recovery of California sea otters. *Ecography* 41, 1751–1762
57. Logan, R.K. and Lowe, C.G. (2019) Space use and inferred spawning activity of three exploited gamefish species on a large artificial reef. *Fish. Manag. Ecol.* 26, 558–569
58. Hamilton, S.L. and Caselle, J.E. (2015) Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proc. R. Soc. B Biol. Sci.* 282, 20141817
59. Selden, R.L. *et al.* (2017) Protection of large predators in a marine reserve alters size-dependent prey mortality. *Proc. R. Soc. B Biol. Sci.* 284, 20161936
60. Alonzo, S.H. *et al.* (2008) The importance of incorporating protogynous sex change into stock assessments. *Bull. Mar. Sci.* 83, 163–179
61. Negrín Dastis, J.O. *et al.* (2018) A fish-mediated trophic cascade on freshwater calanoid copepod abundance is concealed by food web fatty acid availability, functional traits and population sex ratio. *J. Plankton Res.* 40, 197–208
62. Hoy, S.R. *et al.* (2015) Age and sex-selective predation moderate the overall impact of predators. *J. Anim. Ecol.* 84, 692–701
63. Gervasi, V. *et al.* (2015) Body mass relationships affect the age structure of predation across carnivore–ungulate systems: a review and synthesis. *Mammal Rev.* 45, 253–266
64. Boukal, D.S. *et al.* (2008) Does sex-selective predation stabilize or destabilize predator–prey dynamics? *PLoS One* 3, e2687
65. Takyi, E.M. *et al.* (2024) Sex-biased predation and predator intraspecific competition effects in a prey mating system. *AIMS Math.* 9, 2435–2453
66. Poore, A.G.B. *et al.* (2018) Nest building by a small mesograzer limits blade size of the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 165, 184
67. Andrew, N.L. and Jones, G.P. (1990) Patch formation by herbivorous fish in a temperate Australian kelp forest. *Oecologia* 85, 57–68
68. Sikkel, P.C. (1988) Factors influencing spawning site choice by female garibaldi, *Hypsypops rubicundus* (Pisces: Pomacentridae). *Copeia* 1988, 710–718
69. Sikkel, P.C. (1995) Effects of nest quality on male courtship and female spawning-site choice in an algal-nesting damselfish. *Bull. Mar. Sci.* 57, 682–689
70. Hoelzer, G.A. (1990) Male-male competition and female choice in the Cortez damselfish, *Stegastes rectifraenum*. *Anim. Behav.* 40, 339–349
71. Roma, J. *et al.* (2021) Moderately elevated temperatures increase macroalgal food consumption in two sea urchin species from coastal waters of Madeira. *J. Exp. Mar. Biol. Ecol.* 542–543, 151603
72. Cruz-Rivera, E. and Hafez, T. (2022) Sex, mate guarding, and reproductive state as potential modulators of herbivory in an aquatic consumer. *Aquat. Sci.* 85, 12
73. Herre, E.A. (1985) Sex ratio adjustment in fig wasps. *Science* 228, 896–898
74. Smith, G.P. *et al.* (2019) Sex differences in pollinator behavior: patterns across species and consequences for the mutualism. *J. Anim. Ecol.* 88, 971–985
75. Bravo, C. *et al.* (2016) Dietary divergence in the most sexually size-dimorphic bird. *Auk* 133, 178–197
76. Steneck, R.S. *et al.* (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29, 436–459
77. Eger, A.M. *et al.* (2024) The Kelp Forest Challenge: a collaborative global movement to protect and restore 4 million hectares of kelp forests. *J. Appl. Phycol.* 36, 951–964
78. Leal, P.P. *et al.* (2017) Ocean acidification and kelp development: reduced pH has no negative effects on meiospore germination and gametophyte development of *Macrocystis pyrifera* and *Undaria pinnatifida*. *J. Phycol.* 53, 557–566
79. Oppliger, V. *et al.* (2011) Sex ratio variation in the *Lessonia nigrescens* complex (laminariales, Phaeophyceae): effect of latitude, temperature, and marginality. *J. Phycol.* 47, 5–12
80. Korabik, A.R. *et al.* (2023) Examining the reproductive success of bull kelp (*Nereocystis luetkeana*, Phaeophyceae, Laminariales) in climate change conditions. *J. Phycol.* 59, 989–1004
81. Veenhof, R.J. *et al.* (2022) Kelp gametophytes in changing oceans. In *Oceanography and Marine Biology: An Annual Review* (Hawkins, S.J. *et al.*, eds), pp. 335–372, Taylor & Francis
82. Krumhansl, K.A. *et al.* (2016) Global patterns of kelp forest change over the past half-century. *Proc. Natl. Acad. Sci. U. S. A.* 113, 13785–13790
83. Arafeh-Dalmau, N. *et al.* (2020) Marine heat waves threaten kelp forests. *Science* 367, 635
84. Cornelissen, T. and Stiling, P. (2005) Sex-biased herbivory: a meta-analysis of the effects of gender on plant–herbivore interactions. *Oikos* 111, 488–500
85. Romero-Pérez, A. *et al.* (2020) Sex-biased herbivory and its effects on tritrophic interactions. In *Evolutionary Ecology of Plant–Herbivore Interaction* (Núñez-Farfán, J. and Valverde, P.L., eds), pp. 173–189, Springer International Publishing
86. Kabir, Md.F. *et al.* (2014) Plant-sex-biased tritrophic interactions on dioecious willow. *Ecosphere* 5, art153
87. Nifong, J.C. *et al.* (2015) Size, sex and individual-level behaviour drive intrapopulation variation in cross-ecosystem foraging of a top-predator. *J. Anim. Ecol.* 84, 35–48
88. Trillmich, F. *et al.* (2018) Understanding the evolution of personality requires the study of mechanisms behind the development and life history of personality traits. *Biol. Lett.* 14, 20170740

89. Nakazawa, T. (2020) Species interaction: revisiting its terminology and concept. *Ecol. Res.* 35, 1106–1113
90. Gissi, E. *et al.* (2023) Exploring climate-induced sex-based differences in aquatic and terrestrial ecosystems to mitigate biodiversity loss. *Nat. Commun.* 14, 4787
91. Pape, M. *et al.* (2024) Sex contextualism in laboratory research: enhancing rigor and precision in the study of sex-related variables. *Cell* 187, 1316–1326
92. Englund, G. and Leonardsson, K. (2008) Scaling up the functional response for spatially heterogeneous systems. *Ecol. Lett.* 11, 440–449
93. McLaughlin, J.F. *et al.* (2023) Multivariate models of animal sex: breaking binaries leads to a better understanding of ecology and evolution. *Integr. Comp. Biol.* 63, 891–906
94. Bowyer, T.R. (2022) *Sexual Segregation in Ungulates. Ecology, Behavior, and Conservation* (1st edn), Johns Hopkins University Press