That species must differ ecologically is often viewed as a fundamental condition for their stable coexistence in biological communities. Yet, recent work has shown that ecologically equivalent species can coexist when reproductive interactions and sexual selection regulate population growth. Here, we review theoretical models and highlight empirical studies supporting a role for reproductive interactions in maintaining species diversity. We place reproductive interactions research within a burgeoning conceptual framework of coexistence theory, identify four key mechanisms in intra- and interspecific interactions within and between sexes, speculate on novel mechanisms, and suggest future research. Given the preponderance of sexual reproduction in nature, our review suggests that this is a neglected path towards explaining species diversity when traditional ecological explanations have failed.

Species Coexistence: Ecological Differences and Reproductive Interactions

Are ecological differences necessary for species to coexist? Most theoretical and empirical studies of species coexistence (see Glossary) have focused on how canonical ecological differences, such as resource partitioning [1,2], predator avoidance strategies [3], mutualistic associations [4], phenological differences [5,6], and other mechanisms [7,8], underlie coexistence. Yet, a striking feature of many communities is species that seemingly differ little ecologically. Examples include plankton [9], some African lake cichlids [10], new world warblers [11,12], Hyalela amphipods [13], green lace wings [14], Enallagma damselflies [15–17], and the many groups of cryptic species complexes [18](Figure 1). While the strict ecological equivalence of species in these examples has not been empirically tested (but see [19]), earlier work suggested that assemblages of such ecologically similar species are inherently unstable [12,20]. Are these species merely on a delayed stochastic march to exclusion, or are other non-ecological mechanisms potentially stabilizing their coexistence?

To address this question, let us first examine the criteria that must be met for coexistence. Coexistence implies that species can maintain a population under the ecological conditions that they experience at a given location. The most widely used criterion for stable local coexistence is to evaluate if each species in an assemblage can increase when rare and all other species are at their demographic steady states in its absence, the invasibility criterion [7,19,21,22] (Box 1). If all species can mutually invade under such conditions, those species are coexisting. Invasibility occurs because species have demographic advantages when rare (negative frequency dependence), but population regulatory forces increase as any one species’ frequency increases. Recent methods can also identify coexisting species at a stationary state that is not necessarily a point equilibrium [23,24]. While invasibility is a common theoretical criterion, it is very difficult to evaluate in practice [25]. Also, some mechanisms may cause species to have lower population growth rates when rare than when common (i.e., Allee effects [26,27]). In such cases, species can experience positive frequency dependence, which can promote coexistence at regional,
Figure 1. Examples Where Reproductive Interactions are Implicated in Species Coexistence. (A) The fig-pollinating wasp Plistodontes imperialis. Cryptic species of fig-pollinating wasps could locally coexist due to female-biased sex allocation when rare. (B) The damselfly Calopteryx splendens. This species is thought to coexist with the congeneric C. virgo through male–male competition. (C) The jewelflower Streptanthus breviflorus. Interspecific reproductive interaction between sexes could be preventing local, but promoting regional, coexistence with S. hesperidis. (D) The new world warbler (Sethophaea fusca). New world warblers are ecologically similar species in which interspecific male–male competition could be promoting coexistence. (E) The Lake Tanganyka cichlid Petrochromys polyodon. Strong intraspecific male competition for breeding territories is believed to facilitate coexistence with ecologically similar cichlid species. Photo credits: (A) James Cook, (B) Jean-Daniel Echenard, (C) Vernon Smith, (D) William H. Majoros, and (E) Tetsumi Takahashi.

Box 1. The Invasibility Criterion and Reproductive Interactions

Invasibility is a common, but not the only, criterion, used to evaluate species coexistence, whether the species has a positive per capita population growth rate when rare and with all the other species at their long-term demographic steady states. If this criterion is not met, the species is being maintained by other means, such as dispersal, or is on an extinction trajectory. Invasibility is a standard test for coexistence in theoretical models of multispecies interactions [19,22] because it implies long-term persistence of community members via stable point equilibria, limit cycles or chaos, or long-term persistence under temporal stochasticity [1,7].

Ideally, tests of the mechanisms we explore (see Table 1 in main text) are conducted in study systems where invasibility criteria could be evaluated, where sexual selection or other reproductive interactions are suspected to mediate per capita population growth, and where the contribution of these mechanisms to invasibility could be determined. Evaluating invasibility in communities in the field is often logistically challenging, but many of the mechanisms we propose could be tested in the lab or in semi-natural conditions. For example, aphids, bean beetles, Drosophila, and Daphnia can all be reared in experimental settings conducive to testing invasibility [89], and these are also taxa where sexual selection is known to operate. The unique reproductive biology of some organisms may make for especially strong tests of invasibility through reproductive mechanisms where sexual selection and conflict can be reduced (e.g., by enforcing monogamy in some populations and allowing polygyny in others) or by comparing sexual and asexual strains of some species (e.g., Daphnia or aphids).

One complication is that reproductive mechanisms could act in tandem with ecology. Thus, understanding the relative contribution of reproductive mechanisms relative to ecological differences is needed (see Box 2 and Outstanding Questions). The potential for ecology to act could be removed or greatly minimized by experimentally creating conditions so that ecological differences are essentially removed [35]. It may also be possible to estimate changes in fitness proxies related to sexual selection (i.e., mating success) relative to viability selection and then quantify if sexual-selection proxies contribute more than viability selection during invasibility tests. This could be accomplished by developing and empirically parameterizing models that incorporate sex-specific differences in demography [100] and coexistence that use the chain rule to decompose invasibility into the contributions of demography related to ecological relative to non-ecological reproductive mechanisms.
not local, scales, a point we discuss later. Critically, nothing in the various criteria developed for determining if species are coexisting states that species must differ ecologically [28]. Here, we examine an alternative pathway towards coexistence and the maintenance of species diversity, **reproductive interactions**.

At present, the study of reproductive interactions shaping species coexistence is more advanced theoretically than empirically. However, we review empirical evidence when this exists. While our focus is on reproductive interactions promoting coexistence, we end by examining how reproductive interactions may hinder coexistence. Note that reproductive interactions are, of course, ecological in some way or have ecological consequences; but, we mean to emphasize their distinction from canonical ecological differences that are typically thought to underlie coexistence (analogous to reproductive vs. ecological character displacement). Overall, we contend that greater attention to the way coexistence mechanisms can vary across life stages is required to better understand what maintains species diversity beyond what is expected from ecologically based explanations alone (Box 2). Given the importance of community ecology in applied sciences, such as conservation biology and species management, full consideration of reproductive interactions as a mechanism maintaining species diversity is warranted.

**Conceptual Framework: A Place for Reproductive Interactions in Coexistence Theory**

Reproductive interactions, the behaviors associated with mate acquisition (e.g., mate choice or mate competition), can affect species demography in a frequency-dependent fashion. If success in mate acquisition is further shaped by variation in phenotypes, this can generate **sexual selection**. Although sexual reproduction alone is insufficient to promote coexistence, the balance struck in the outcome of reproductive interactions between conspecifics and heterospecifics can affect demographic rates that shape coexistence. Notably, this can occur in the absence of any ecological differences defined by resource-based or consumer–resource interactions (Table 1).

**Theoretical Predictions and Empirical Evidence of Reproductive Interactions Shaping Species Coexistence**

Reproductive interactions are often assumed to only affect demography through conspecific male and female interactions. However, there are at least four different paths in which reproductive interactions can occur, intraspecific and interspecific interactions within and between the sexes (Figure 2). These paths encompass the diversity of reproductive interaction mechanisms acting within and between species (Table 1). We note that the terminology of reproductive interactions can be confusing, as different terms have been used to describe the same phenomena. Heterospecific male–male competition and male–female interactions have often been referred to as reproductive interference [29–35]. Because the consequences of these interactions for species coexistence differ, we recognize them as distinct. Similarly, conspecific male competition has been referred to as male–male repulsion, male attacks, and aggression [36–38]; we simply call it intraspecific male–male competition. Later, we discuss theoretical underpinnings of each mechanism, what empirical studies have revealed, where deficiencies lie, and how the demographic consequences can work in a fashion similar to ecological mechanisms of coexistence.

**Mechanism 1: Intraspecific Interactions Between Sexes**

**Theoretical Studies**

The effect of intraspecific male–female interactions in species coexistence has been theoretically studied in two contexts, female mate choice [39] and **sexual conflict** [40,41]. A model...
Box 2. Coexistence Mechanisms Can Shift between Life Stages

Many species pass through multiple life stages as they complete their life cycle, a fact that researchers should not ignore when examining the potential for species to coexist. Indeed, the presence of unique life stages provides an opportunity for different coexistence mechanisms to operate at different life stages [101,102]. For example, the effects of resource competition or differential predation during the juvenile stage could be counterbalanced, reversed, or intensified by reproductive interactions during the adult life stage [103]. In a similar vein, some species might only have an opportunity for reproductive mechanisms to arise in certain geographic locations (e.g., migratory birds). Thus, there may also be a geographic component to ontogenetic shifts in coexistence mechanisms, and this may partly determine the spatial scale of species coexistence [104]. As a result, species could be ecologically equivalent during the juvenile stage, but reproductive interactions during the adult stage could be sufficient to promote coexistence (Figure I). Yet, empirical studies have largely ignored the potential for coexistence to emerge at different life stages where the reproductive mechanisms noted earlier have a role [105]. Neglecting the different life stages can increase the risk of false positives and false negatives for detecting coexistence (Figure I). Experiments manipulating species frequencies during different life stages and measuring the fitness consequences on survival and mating success are thus a necessary step. Given that different mechanisms do not contribute equally to population growth, as long as reproductive interactions have the largest effect on population growth rate, they will be a key mechanism promoting or preventing species coexistence. Sensitivity or elasticity analyses (measuring the effect in population growth as an absolute or proportional change in individual fitness components, respectively) would be invaluable in evaluating the relative importance of the mechanisms operating at different life stages [103,106–109]. Because two stably coexisting species will have a mean population growth rate of zero on the long term, an analysis of the sensitivity of equilibrium abundances is required [110]. For a two-species model with ontogenetic shifts, see [24].

Figure I. Species Interactions Can Have Different Consequences for Frequency Dependence in Different Life Stages. Neglecting life stages can lead to false positives, when negative frequency dependence (e.g., adult stage) is counteracted in different life stages (e.g., juvenile stage), and false negatives, when negative frequency dependence is achieved by the total effect of species interactions in all life stages. The extent to which these contrasting outcomes of coexistence emerge across life stages requires empirical testing.

studying the coexistence of ecologically equivalent species differing only in secondary sexual characters used in female mate choice showed that species were unable to locally coexist [39]. However, in patchy environments, mate search costs could facilitate regional coexistence because if females move to an area occupied mostly by heterospecics, their fitness would decline due to the costs of not finding a preferred male [39]. This creates a priority effect, generating positive frequency-dependent selection and creating a situation where different species dominate different patches. Species coexistence is then manifested regionally [39].
The role of sexual conflict in species coexistence has been explored in two theoretical studies showing that it can promote stable local coexistence even when species are ecologically equivalent. In these models, sexual conflict reduces female survival [41] and fecundity [40] in a density-dependent fashion. Thus, when intraspecific density increases, male–female encounters are more common and sexual conflict intensifies, reducing female fitness and population growth.

**Table 1. Predictions and Core Assumptions of Theoretical Studies Testing the Role of Reproductive Interactions on Species Coexistence**

<table>
<thead>
<tr>
<th>Interaction</th>
<th>Mechanism</th>
<th>Predictions</th>
<th>Assumptions*</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intraspecific between sexes</td>
<td>Female mate choice</td>
<td>Regional coexistence</td>
<td>Patchy environment, mate search costs</td>
<td>[39]</td>
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<tr>
<td></td>
<td>Male mate choice</td>
<td>Not studied</td>
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<tr>
<td></td>
<td>Sexual conflict</td>
<td>Local coexistence</td>
<td>Male mating harassment has a negative effect on female fitness</td>
<td>[40,41]</td>
</tr>
<tr>
<td>Interspecific between sexes</td>
<td>Heterospecific matings</td>
<td>Local exclusion, regional coexistence</td>
<td>Patchy environment and habitat segregation</td>
<td>[50,51]</td>
</tr>
<tr>
<td>Intraspecific within sexes</td>
<td>Male–male competition</td>
<td>Local coexistence through spatial separation (due to territoriality) and sex allocation</td>
<td>Stronger aggression to conspecifics. Female-biased sex allocation when rare</td>
<td>[37,38,54,56–58]</td>
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<td></td>
<td>Female–female competition</td>
<td>Not studied</td>
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<td>Interspecific within sexes</td>
<td>Male–male competition</td>
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<td></td>
<td>Female–female competition</td>
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*Additional assumptions are inherent to each model, so the reader should carefully evaluate them. Those provided here are meant to guide the reader in evaluating the potential suitability of a particular model for their system.

The role of sexual conflict in species coexistence has been explored in two theoretical studies showing that it can promote stable local coexistence even when species are ecologically equivalent. In these models, sexual conflict reduces female survival [41] and fecundity [40] in a density-dependent fashion. Thus, when intraspecific density increases, male–female encounters are more common and sexual conflict intensifies, reducing female fitness and population growth.
rates. Sexual conflict then generates negative frequency dependence, giving each species an advantage when rare, promoting species coexistence [40,41].

**Empirical Evidence**

To date, there is no definitive evidence for either mate choice or sexual conflict promoting species coexistence. M’Gonigle et al. [39] argue that female mate choice could explain the high diversity of seemingly ecologically equivalent species, such as some cichlid fish (Figure 1). Sexual conflict, however, is known to reduce female fitness and population viability [30,42], and the intensity of sexual conflict increases with density [30]. However, sexual conflict has not been empirically studied in the context of species coexistence and remains a promising mechanism to explore.

Although we have focused on female mate choice, male mate choice also occurs [43–45] but has not been studied, empirically or theoretically, in the context of species coexistence. This is surprising because male mate choice can enhance female fitness [43,45,46] with potentially important demographic consequences. For example, male mate choice can occur when males present females with nuptial gifts (e.g., male scorpionflies (*Panorpa cognata*) produce a salivary mass that females consume and they produce larger gifts to higher-quality females [47]) or by approaching good condition females in sexually cannibalistic species [48]. Male mate choice in these examples is interesting, as reproductive and foraging success are linked. Therefore, increased encounter rate between males and preferred females can increase female fitness while avoiding or reducing the costs of sexual conflict, causing positive frequency dependence and facilitating regional, but not local, species coexistence.

**Mechanism 2: Interspecific Interactions between Sexes**

**Theoretical Studies**

Heterospecific male–female interactions (e.g., inviable hybrid production, mating attempts, reproductive interference) are costly, especially to females [49]. However, if females can avoid habitats with high heterospecific densities, regional coexistence of ecologically identical species can occur if females suffer higher costs when rare (i.e., more heterospecifics), leading to positive frequency dependence. If females decide to avoid patches with too many heterospecific males, this can lead to conspecific aggregation. This conspecific aggregation can enable the coexistence of ecologically identical species in a region [50] because conspecific aggregation both reduces hybridization and causes the population to be regulated by conspecific density alone (rather than frequency) [51].

**Empirical Evidence**

The costs of heterospecific male–female interactions are often frequency dependent. For example, experiments with *Leptidea* butterfly species that exhibit habitat segregation showed that females often fail to mate with conspecifics in the presence of heterospecific males that court indiscriminately, avoiding hybridization at the cost of reduced mating, especially when heterospecifics are abundant [52]. Habitat segregation as a result of heterospecific reproductive competition (e.g., competition for pollinators) has also been shown in *Streptanthus* plants [53]. Interestingly, this study shows a disadvantage when rare, but if a frequency threshold is reached, species can escape the costs of being rare [53] (i.e., causing an Allee effect). Whether such habitat segregation and aggregation in these systems leads to stable species coexistence is still unknown.

So far, we have presented heterospecific reproductive interactions between sexes as only costly to females; however, they may also be costly for males. If and how heterospecific
reproductive interactions can be costly for males in a way that affects population growth rate in a frequency-dependent fashion is still an open question.

**Mechanism 3: Intraspecific Interactions Within Sexes**  
**Theoretical Studies**

The effect of intraspecific interactions within sexes in coexistence have only been studied through male–male competition, either by spatial separation via territoriality or sex allocation. The spatial separation hypothesis states that aggressive interactions for mating territories is stronger between conspecifics than with heterospecifics, even if both species have identical ecological habitat requirements [38]. Stronger competition between conspecifics can lead to stronger aversion (e.g., more distant territories), thereby allowing heterospecifics to occupy the areas between conspecific territories [38]. As a result, competition with conspecific neighbors decreases population growth as they become common, leading to negative frequency dependence and preventing species exclusion [37,38,54].

The sex allocation hypothesis states that species increasing the production of females would increase the population growth rate. In species that evolved anisogamy, reproduction is limited by the number of females or female gametes (e.g., in plants) [55]. Plants have often been used to illustrate this idea. If pollen production is high, pollen competition would increase, and mating success per pollen grain would decrease. Therefore, investing more in seeds would create more mating opportunities and therefore increase population growth rates [56,57]. Yet, for sex allocation to promote coexistence, female production must increase at low frequencies, providing a demographic advantage when rare [41,56–58]. But why would species have female-biased sex allocation only when rare? One argument is that the identity of the conspecific competitors matters [58]. At low species frequencies, competition for mates is more likely to occur between male siblings. Increasing the production of females would reduce sibling competition and increase maternal fitness [58]. Species, however, must be able to adjust sex allocation at a similar or faster rate than demographic changes. Given the myriad of requirements that must be met for sex allocation to occur in a way that can promote coexistence (e.g., the speed at which females can adjust sex allocation, relatedness of individuals), the viability and generality of this mechanism is questionable.

**Empirical Evidence**

Partial empirical support for the hypothesis of intraspecific male–male competition creating spatial separation that facilitates coexistence comes from territorial cichlid fish (*Petrochromis* spp.). *Petrochromis* males attack and chase conspecifics farther away from their territories, while they only chase heterospecifics out of their immediate territory. Therefore, conspecific territories do not share borders, and heterospecific males establish themselves in between conspecific territories [37,54]. A more recent study showed that increased competition at high conspecific densities reduced male longevity in *Calopteryx* damselflies [35] (Figure 1). Notably, the later study was conducted so that potential ecological differences were essentially removed. However, for male–male competition to facilitate coexistence, the negative effect of male–male competition on male fitness has to be large enough to affect population growth. Currently, it is not known if increased intraspecific male–male competition can alone reduce population growth, although it is important to note that different reproductive interactions often act together (e.g., male competition and female choice). Therefore, male–male competition can affect coexistence indirectly by affecting other types of interactions.

Empirical studies evaluating the sex allocation hypothesis are rare. Arguably, the best evidence comes from cryptic, haplodiploid species of fig-pollinating wasps (Agaonidae) (Figure 1). Females
of such wasp species (foundress) oviposit inside the fig inflorescence [59] and can manipulate offspring sex ratio allocation [59,60]. One study showed that usually only one foundress of each species is responsible for the brood of each fruit, and that the sex ratio of the species at low frequency was female biased [59]. However, species frequency was evaluated at a regional scale (e.g., total wasp abundance), while competition and mating were examined at a local scale (e.g., inside the fruit). Because one foundress of each species is responsible for the brood of each fruit, the species frequency experienced inside the fruit may be different than when pooled from multiple fruits. Moreover, evidence that lower densities increase female sex allocation is mixed. For example, in red deer (Cervus elaphus) and great tits (Parus major), male offspring production increases at low densities and female production decreases [61,62].

Intraspecific female–female competition has not been studied theoretically or empirically in the context of species coexistence. A prime system to study the role of female mate competition in community ecology is sympatric species with sex role reversal, such as Phalaropus fulicarius and P. lobatus [63]. In such systems with female mate competition, dominant females could monopolize males and prevent subdominant females from reproducing, which would reduce the number of fertilized females. When common, females would not be able to monopolize all males, increasing the proportion of fertilized females and leading to increased population growth rate (i.e., positive frequency dependence), which could prevent local coexistence. Another potential system is species with mate cannibalism [64] as females consuming their mates would limit the number of available males, increasing competition for both mates and resources (both of which would be the males). This effect could be enhanced in the presence of male mate choice, such that a few preferred females copulate with and consume a larger proportion of males. In such a case, female competition could increase the costs for nonpreferred females at low frequency, increasing the chance of exclusion.

Mechanism 4: Interspecific Interactions Within Sexes
The role of heterospecific male mate competition in species coexistence has not been theoretically studied; however, empirical studies exist. Heterospecific male aggression is expected to be pervasive among recently diverged species (with little or no phenotypic differentiation that might yield ecological differences) because for males, the cost of heterospecific matings is lower than missing a mating opportunity. As a result, males of closely related species frequently compete for every mating opportunity with both conspecifics and heterospecifics [29,65]. A study with 330 species of Amazonian birds found that interspecific aggression for mating or breeding territories was common between congeneric species [66], and a study of 49 species of wood warblers found that at least 19 showed aggression to other wood warblers [67]. The effect of interspecific male–male competition in species coexistence could occur indirectly through its effect on male–female interactions. For example, if heterospecific competition reduces sexual conflict by limiting access to conspecific females [30] or reducing male survival [35], this can in turn increase female fitness in a frequency-dependent fashion. Although the earlier findings are suggestive, they have not fully evaluated the ecological equivalence of species or tested the role of interspecific competition within sexes (either male–male or female–female competition) in species coexistence.

Paths Forward Towards Understanding the Contribution of Sexual Selection in Species Coexistence
We have highlighted several knowledge gaps of how and when reproductive interactions can promote or prevent coexistence (Table 1). Importantly, reproductive interactions can promote
coexistence even if species are ecologically equivalent, but they can also promote coexistence in ecologically different species as long as the effect of reproductive interactions on population growth rate is larger than the effect of ecologically based interactions (Box 2). Many of these mechanisms also deserve additional theoretical scrutiny. Beyond those gaps, we highlight four additional priority questions to better understand the contribution of reproductive interactions and sexual selection as coexistence mechanisms (also see Outstanding Questions).

What are the Contributions of Evolution to Species Coexistence?
Evolutionary processes are increasingly recognized as having a role in species coexistence [68–72]; but this line of work has focused almost solely on ecological aspects of natural selection. Reproductive interactions are frequently shaped by sexual selection, which, by extension, suggests that evolution of traits explicitly linked to mating success, and not ecological interactions, can influence coexistence. Examples include traits involved in female choice [73], repeated mating attempts [74], copulation [16], mate competition [75], or species discrimination [76]. Such traits often experience rapid evolution [77]. If evolution of these traits intensifies demographic responses to conspecifics relative to heterospecifics, this can promote coexistence [28,78]. For example, local adaptation can mediate the strength of reproductive interactions [29,76,79,80] and thus the strength of intraspecific competition [81]. Moreover, local adaptation can affect the strength of frequency dependence in intraspecific competition [81] and promote coexistence [78]. Indeed, recent work suggests that adaptation to intraspecific competition can lead to the evolution of traits that confer higher individual fitness at the cost of population fitness, which defines population growth rate. Because competition is density dependent, adaptation to conspecifics can promote coexistence [82].

The strength of reproductive interactions, and their importance relative to ecological differences in species coexistence, may depend on species shared macroevolutionary history. Closely related species are more likely to be phenotypically similar [83], potentially recognizing each other as suitable mates, leading to stronger interspecific reproductive interactions [29,66]. This could mean that interspecific reproductive interactions are more likely to affect species coexistence in recently diverged species. If so, this may provide a mechanism promoting the coexistence of species that do not (or are yet to) diverge ecologically. Given that reproductive isolation can lead to speciation and that traits mediating reproductive interactions often evolve more rapidly than ecological characters [77,84], it may be that divergence in reproductive characters occurs rapidly enough to promote coexistence, independently of the evolution of ecological differences. Indeed, some of the most rapidly diversifying clades show little to no ecological differentiation [85–87], and these may be prime candidates where reproductive mechanisms may be most relevant.

How Do Interactions between Ecology and Sexual Selection Shape Coexistence?
While we have been concerned throughout with ecologically equivalent species, this does not mean ecology is irrelevant [28]. Reproductive interactions and the potential for sexual selection are embedded within an ecological context that may constrain or promote coexistence. For example, theoretical and empirical work shows that sexual conflict is weaker in poorly adapted populations where selection for adaptation to local environmental conditions is strong, while in well-adapted populations, such selection is relaxed and sexual conflict intensifies [79,80]. If sexual conflict promotes coexistence [40,41], species could be found in a mosaic of co-occurring and coexisting populations, depending on how adapted they are [88]. Thus, a tension between ecologically driven local adaptation and sexual selection promoting coexistence may exist. More generally, linking sexual selection and sexual conflict in an eco-evolutionary context underlying coexistence remains a major unresolved challenge.
How Does Plasticity in Sexual Traits Contribute to Coexistence?

Just as phenotypic plasticity in ecologically relevant traits is expected to affect species coexistence [89], plasticity can also affect traits involved in reproductive interactions [90,91]. Unlike evolution, which acts between generations, phenotypic plasticity can generate rapid changes in reproductive behaviors. For example, female Calopteryx damselflies show plastic mate choice in the presence of heterospecifics to a more distinct phenotype from heterospecifics [92]. This plastic female mate preference can reduce costly heterospecific matings and potentially leads to species exclusion. If heterospecifics are common, the females’ plastic responses would reduce costly heterospecific matings and increase fitness in a frequency-dependent fashion. Collectively, this suggests that phenotypic plasticity in traits mediating reproductive interactions would allow species to avoid costly heterospecific interactions, giving time for species to evolve and coevolve. Therefore, plasticity could be especially important for coexistence in scenarios in which new species assemblages are forming, such as during dispersal to more extreme latitudes and higher elevations due to climate change. Further integration between studies of plasticity, sexual selection, and species coexistence are needed to provide a more holistic view of how changes in traits underlying reproductive interactions can promote species coexistence.

When Do Reproductive Interactions Prevent Coexistence?

So far, we have emphasized when reproductive interactions enhance coexistence. However, reproductive interactions can also promote exclusion, and this could occur even if species are ecologically differentiated. As noted earlier, female mate choice can lead to species coexistence at the regional scale, but at the local scale, exclusion is expected as the costs of being rare and not finding conspecific mates would lead to positive frequency dependence [39]. Interspecific interactions between sexes can also lead to species exclusion in the absence of spatial separation or when rare [50,53,93–95]. Fundamentally, if reproductive interactions cause positive frequency dependence and there are no ecological differences between species to counterbalance population growth, exclusion is expected [96]. Similarly, if species are ecologically equivalent but reproductive interactions generate competitive differences, this can alter the outcome from stochastic to deterministic with one dominant species persisting. Determining under what conditions reproductive interactions constrain or facilitate species coexistence will provide critical insight into understanding the maintenance of species diversity.

Concluding Remarks

Ecologists have a keen eye for discerning and describing ways that species differ ecologically to promote coexistence [97]. As a result, much progress has been made in our understanding of how species diversity can be maintained when they interact differently with the environment. Yet, determining the mechanisms promoting species coexistence is an equally important goal [28,98]. Our review of theoretical models and current empirical evidence brings greater attention to the diverse mechanisms, beyond those focused on ecology, that can foster species coexistence and the maintenance of biological diversity (see Outstanding Questions). What we are not advocating though is that coexistence should necessarily be the default [19,20]. There are examples of species that simply do not coexist. Community ecologists must reconcile our perception of differences among species with the development of theoretical, observational, and experimental work designed to understand if ecological differences act to maintain species diversity, if they only slow its erosion, or if other non-ecological mechanisms sustain it. Studies of reproductive interactions and sexual selection may be outside the wheelhouse of many community ecologists, but we suggest that they should be included.

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Declaration of Interests

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References

77. Simmons, L.W. and Fitzpatrick, J.L. (2019) Female genitalia can evolve more rapidly and divergently than male genitalia. Nat. Commun. 10, 1312