Trends in Ecology & Evolution

Opinion

Sexual Dimorphism and Species Diversity: from Clades to Sites

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A variety of relationships have been observed between sexual dimorphism and species diversity, from positive to negative and nonsignificant. Although many hypotheses have been proposed to explain these relationships, it has proven difficult to understand why patterns are so variable. Most studies on this topic have used clades as phylogenetically independent replicates for pattern analysis, but a few recent studies took an alternative approach, using sites as spatially independent replicates. We discuss how the new, site-based studies complement the traditional, clade-based studies and argue that the combined use of the two approaches will be more powerful than either alone in understanding environmental factors that produce variation in sexual dimorphism–species diversity relationships.

Highlights

Sexual dimorphism and species diversity are correlated in various ways, showing positive, negative, and nonsignificant relationships.

To study sexual dimorphism–species diversity relationships (SSRs), clade-based analysis has traditionally been used, asking whether clades that vary in the extent of sexual dimorphism also differ in the extent of speciation and extinction.

By contrast, site-based analysis, which has rarely been used, asks whether sites that vary in the diversity of species belonging to a certain clade also differ in the extent of sexual dimorphism in those species.

We argue here that SSRs can be studied more effectively through the combined use of clade-based and site-based analyses than through either analysis alone.

Linking Two Forms of Biodiversity

Sexual dimorphism (see Glossary) and **species diversity** are two of the most celebrated forms of biodiversity, yet they have been studied separately for the most part. According to a recent Web of Science search, 10 847 and 19 269 papers were published on sexual dimorphism and species diversity, respectively, during the past decade. Of these papers, only 28 mentioned both terms, which is likely to reflect a disciplinary divide: sexual dimorphism (Figure 1A) has been studied by evolutionary ecologists interested in how individual interactions influence the evolution of phenotypes, while species diversity has been studied by community ecologists interested in how species interactions shape the structure of communities.

Despite this disciplinary separation, increasing evidence indicates that the two forms of biodiversity are often corelated in various ways (Figure 1B) [1–21]. Using **clades** as phylogenetically independent replicates, many studies have reported positive relationships: clades that exhibit a large degree of sexual dimorphism tend to contain a greater number of species than those with little sexual dimorphism. In other cases, however, sexual dimorphism–species diversity relationships (SSRs) are negative, with more dimorphic clades having lower species diversity. Cases where no significant relationship is detected are also common. Reasons for this variation, which should interest evolutionary and community ecologists alike, remain unclear.

Research on SSRs has so far been driven primarily by evolutionary ecologists, which perhaps explains why most work has used phylogenetic, clade-based analysis (Figure 1B). Among these papers, a few recent ones are unusual in that they took an alternative, site-based approach [17,19,21], following a community ecology tradition (e.g., [1]). This approach compares multiple sites, focusing on a certain clade that shows among-site variation in both sexual dimorphism and species diversity. These sites can be discrete habitats, like islands and lakes [17,19], or they can be less discrete and more artificially defined, like small areas of a large tract of forest or ocean [21].

Although limited in number, these studies, too, indicate large variation in SSRs (Figure 1B). The earliest study of this kind we are aware of found negative SSRs in *Anolis* lizards on Caribbean islands [1] (see also [22,23]). Negative SSRs were also found in a site-based study on *Liolaemus* lizards in Chile and Argentina [21]. However, a site-based study in cichlid fishes in African lakes suggested positive SSRs [17] and a global site-based analysis of island lizards and carnivorous mammals found positive, negative, and nonsignificant relationships [19].

In this article, we argue that more site-based studies are needed to better understand why patterns are so variable. To develop this argument, we start by briefly reviewing the hypotheses that have been

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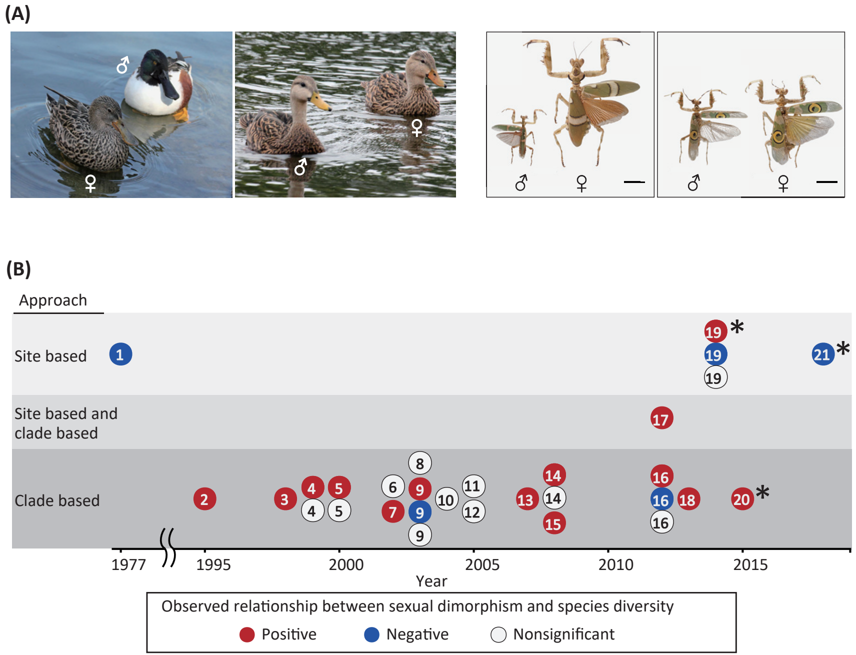

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Figure 1. Organism Examples and Research Chronology on the Relationships between Sexual Dimorphism and Species Diversity.

(A) Examples of differences in the extent of sexual dimorphism between related species. From left to right: Pronounced sexual dichromatism in *Anas clypeata* (northern shoveler); moderate sexual dichromatism in *Anas fulvigula* (mottled duck); pronounced sexual size dimorphism in *Theopropus elegans* (banded flower mantis); and moderate sexual size dimorphism in *Pseudocreobotra ocellata* (African flower mantis). Scale bars for the mantises indicate 1 cm. Photographs: Dick Daniels (ducks) and Rick Wherley, modified from [80] (mantises). (B) Representative studies that used sites, clades, or both as the unit of replication to examine the relationships between sexual dimorphism and species diversity. The studies reported negative (blue circles), positive (red circles), and nonsignificant (white circles) relationships. Numbers in circles correspond to those assigned to the references cited in the main text (i.e., paper 1 is Schoener, 1977 [1], paper 2 is Barraclough *et al*., 1995 [2], etc.). Most studies primarily discussed the effect of sexual dimorphism on species diversity, although a handful of studies (marked with asterisks) explicitly considered the effect of species diversity on sexual dimorphism. To find relevant studies, we used the Web of Science in April 2019 to search for papers that included the following keywords: ('sexual dimorphism' or 'sexual dichromatism') and ('species diversity', 'species number', 'species richness', or 'diversification'). In addition, we reviewed papers that cited or were cited by these papers.

proposed to explain SSRs. Given these hypotheses, we examine why it is difficult to understand variation in patterns of SSRs solely through the clade-based approach. We then discuss how site-based studies can complement clade-based studies (Box 1) and why the combined use of the two approaches can be more effective than either approach alone.

Contrasting Hypotheses

The literature on SSRs is replete with many hypotheses that seem to contradict one another (Figure 2 and Table 1). For example, one way in which sexual dimorphism can affect species diversity is through its effects on **speciation**, but this effect has been hypothesized to be both positive and negative. A long-standing body of theory predicting positive effects (H1 in Figure 2 and Table 1) suggests that **sexual selection** and conflict promote sexual dimorphism, which in turn facilitates speciation [24–33]. In addition, sexual dimorphism may reduce the likelihood of young lineages collapsing back to the same species following secondary contact, thereby facilitating allopatric speciation [9,28,30,34–40], as hypothesized in the 'differential fusion' model [32]. This model may explain, for example, why selection that produces sexual dimorphism in wing color facilitates

Glossary

Adaptive radiation: the evolution of ecological diversity within a rapidly multiplying lineage.
Character displacement: the process by which interspecific or inter-sexual competition drives evolutionary change of characters of the evolving organisms.
Clade: a group of extant species that comprise all of the evolutionary descendants of a common ancestor.
Sexual conflict: the conflict that exists as a result of the divergent evolutionary interests of males and females.
Sexual dimorphism: differences in traits between males and females of the same species.
Sexual selection: a type of selection for traits that increase the reproductive success of an individual. Sexual selection can be considered a subset of natural selection that specifically favors traits associated with mating.
Speciation: the process by which new species form from existing ones during evolution.
Species diversity: the number of species and/or the evenness of the relative abundance of species in a focal clade or site.
Species pool: the regional set of species that can potentially colonize a focal site.

Box 1. Some Common Misconceptions, Difficulties, and Solutions

Clade- and site-based approaches may seem distinct in the response variable they aim to explain. After all, species diversity in a clade encompasses all species in the clade, whereas species diversity at a site refers only to the subset of these species found at that site. However, the two facets of species diversity share basic processes shaping them, including speciation and extinction. Speciation not only contributes to the global diversity of a clade but can also occur within sites, both sympatrically and allopatrically [70,71]. Similarly, extinction can be both global and local, and site-scale local extinctions can collectively result in extinction at the large scales that clade-based studies typically focus on. Factors affecting these processes at global and local scales are therefore not independent of each other. Thus, clade- and site-based approaches are both relevant to all hypotheses in Table 1 in main text.

That said, clade- and site-based analyses can yield seemingly incompatible results owing to differences in the spatial scale at which processes operate. For example, suppose that clade-based analysis indicated that more dimorphic clades were more speciose because of increased speciation (H1), showing a positive SSR. Suppose further that species belonging to these clades were distributed across many local sites. Site-based analysis could reveal a negative SSR if more dimorphic species were less likely to coexist locally because of increased extinction (H4). We can reconcile apparent contradictions like this by acknowledging that the relative importance of speciation and extinction can vary with spatial scale.

One common assumption of clade-based analyses is that each clade can be studied separately from other co-occurring clades. However, even distantly related clades (e.g., newts and aquatic insects [72], plants and plant-associated microbes [73,74]) can affect one another strongly through trophic and other interactions [75,76]. One way to embrace strong inter-clade interactions is to treat non-focal taxa as environmental factors and investigate their effects on the focal clade's SSRs. In some cases, however, inter-clade interactions may be so intricate that sexual dimorphism in one clade (e.g., sticklebacks) affects species diversity in another (e.g., salamanders). In these cases, SSRs can be analyzed at the inclusive phylogenetic scale that encompasses all interacting clades. However, significant SSRs may be detectable only at the generic or even finer scale [32]. To identify the appropriate phylogenetic scales to analyze SSRs, good natural historical knowledge is needed.

speciation in birds [32]. Furthermore, dimorphism-producing selection may increase genetic diversity, which may in turn promote speciation by enabling rapid **adaptive radiation** in local communities [41]. For example, when male and female stickleback fish evolve to be better at capturing benthic and limnetic prey, respectively, this sexual dimorphism in foraging may allow more rapid interspecific radiation into benthic and limnetic ecomorphs than otherwise possible as the fish colonize new lakes [42].

These hypotheses predicting positive effects contrast with an alternative hypothesis (H2); namely, that sexual dimorphism evolves as a result of **character displacement**, which then hinders speciation [43,44]. When resources are limited, inter-sex differences in resource-acquiring traits may enable males and females to specialize on different resources [43,45]. For example, in salamanders, competition appears to induce character displacement between sexes [45] (but see [46]). Similarly, sexual dimorphism in the stickleback's gill raker may also evolve as a result of character displacement [43]. In both cases, dimorphic species each occupy two different feeding niches, decreasing the number of available niches that would otherwise encourage speciation via adaptive radiation. In short, this hypothesis suggests that sexual dimorphism is an alternative outcome to speciation.

In addition to speciation, sexual dimorphism can affect extinction [33]. These effects have also been hypothesized to be both positive and negative. Sexual selection that causes sexual dimorphism may protect species against local extinction (H3) via genetic benefits to populations [47,48], particularly in large populations [49]. For example, Lumley *et al.* [48] showed that in the flour beetle, *Tribolium castaneum*, lineages from populations that had experienced stronger sexual selection were less likely to go extinct because sexual selection reduced mutation load.

However, evidence from birds [50,51], marine ostracods [52], and flowering plants [53] supports the opposing hypothesis that sexual dimorphism increases the risk of local extinction (H4). Increased extinction risk may be due to sexual selection resulting in extravagant traits that increase mortality

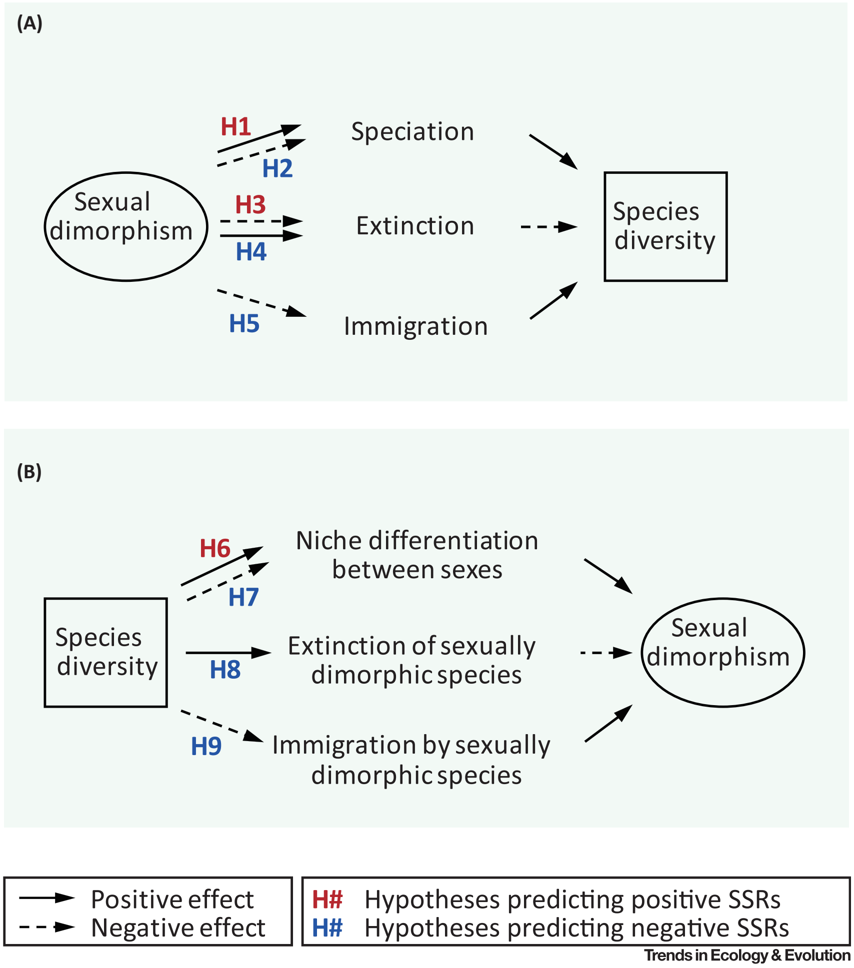

Figure 2. Processes Hypothesized to Shape Sexual Dimorphism–Species Diversity Relationships (SSRs). (A) Effects of sexual dimorphism on species diversity. (B) Effects of species diversity on sexual dimorphism. Unbroken and broken arrows denote positive and negative effects, respectively. Hypothesis numbers (H1 to H9) correspond to those in the main text and in Table 1.

rate [26,54] or, in the case of plants, the effects may be due to misrecognition of plant partners by pollinators [53]. Furthermore, if sexes and species are rival units in resource competition [21], higher sexual dimorphism at a local site can result in more scarcely available resources for heterospecific individuals at that site, which can then increase the rate of local extinction and reduce the chance of successful immigration (H5). This zero-sum game, where either a large degree of sexual dimorphism or a large number of species can arise, would cause a negative association between sexual dimorphism and species diversity [21].

To further complicate matters, causation can go in the other direction, with species diversity affecting sexual dimorphism (Figure 2 and Table 1), and these effects have also been hypothesized to be both positive and negative. They may be positive (H6) when both sexes and species compete for the same resources [43,45,55–57]. In these cases, increasing the number of species may intensify competition, which can in turn increase the selection pressure for evolutionary divergence of resource-acquiring traits between sexes. However, for the same reasons as for H2 [43,44], species diversity may instead inhibit sexual dimorphism (H7) if sexes and species are alternative units for character displacement. Similarly, for the same reasons as for H5 [21], species diversity may

Table 1. Hypotheses Proposed to Explain the Relationships between Sexual Dimorphism and Species Diversity

Hypothesis number[a]	Prediction	Expected SSR	Mechanisms	Refs[b]
Effects of sexual dimorphism on species diversity				
H1	Sexual dimorphism promotes speciation	Positive	Sexual selection facilitates speciation	[24]
			Sexual conflict facilitates speciation	[25,35]
			Sexual dimorphism drives ecological speciation	[26,29]
			Maintenance of species after secondary contact	[32,35]
			Increased genetic diversity	[42]
H2	Sexual dimorphism inhibits speciation	Negative	Sexes and species as alternative units for character displacement	[43,44]
H3	Sexual dimorphism inhibits extinction.	Positive	Sexual selection accelerates adaptation	[47,49]
			Sexual selection purges mutation load	[48]
H4	Sexual dimorphism promotes extinction	Negative	Costly extravagant traits	[26,51,53]
			Reduced population size increases demographic stochasticity	[49]
			Sexes and species as rival units for niche use	[21]
H5	Sexual dimorphism inhibits immigration	Negative	Sexes and species as rival units for niche use	[21]
Effects of species diversity on sexual dimorphism				
H6	Species diversity promotes niche differentiation between sexes	Positive	Disruptive selection, causing inter-sex trait divergence	NA[c]
H7	Species diversity inhibits niche differentiation between sexes	Negative	Sexes and species as alternative units for character displacement	[43,44]
H8	Species diversity promotes extinction of sexually dimorphic species	Negative	Sexes and species as rival units for niche use	[21]
H9	Species diversity inhibits immigration by sexually dimorphic species	Negative	Sexes and species as rival units for niche use	[21]

[a] Hypothesis numbers correspond to those in Figure 2.

[b] Representative references are cited. The list is not exhaustive.

[c] No reference was identified, but this hypothesis is discussed as a possibility in the main text.

inhibit sexual dimorphism if sexes and species are rival units in terms of extinction (H8) and immigration (H9).

Clade-Based versus Site-Based

These hypotheses, as well as the similarly variable patterns of SSRs that have been reported (Figure 1B), indicate that a fundamental challenge is to understand when positive and negative SSRs are expected. What are the environmental conditions under which positive SSRs emerge and what are those under which negative ones do? More empirical data are needed before we can fully address these questions, and we suggest that addressing them would be hard if we continue to use only the conventional, clade-based approach. We argue that it is more productive to use both the clade-based and the site-based approach as they are complementary.

To make this argument, it helps to first compare the pros and cons of the two approaches. The strength of the clade-based approach is that it makes use of the variation among clades that has been formed over long evolutionary time [20,33]. Consequently, the approach allows one to holistically investigate the net effect on SSRs of all factors that have influenced speciation, extinction, immigration, and inter-sex niche differentiation. The rapidly improving phylogenetic resolution afforded by new molecular data [58,59] – coupled with increasingly sophisticated methods using these data to reconstruct lineage history and estimate speciation and extinction rates [60–62] – is making the clade-based approach more and more powerful [20,33].

However, the difficulty is that clades, even when well-resolved, are hard to compare because the geographical ranges of many clades are too large for their environmental conditions to be characterized in adequate detail. This uncertainty limits the analysis of SSRs because sexual dimorphism is not the only factor that affects species diversity and various environmental conditions that vary over space may alter the importance of sexual dimorphism relative to other factors. In addition, environmental conditions may determine which of the opposing mechanisms (Figure 2) operate.

The flip side of this limitation of the clade-based approach is the strength of the site-based approach; namely, that the effects of local environmental conditions on SSRs can be investigated more directly by site-based analysis [17,21]. There are three interrelated reasons for this strength. First, sites can be chosen so as to be statistically independent from one another in terms of both the drivers being tested for (i.e., local environmental factors) and the response variables being examined (i.e., sexual dimorphism and species diversity). This is in contrast to clades, which often overlap with one another in their geographical ranges. When they overlap substantially, it can be difficult to secure replicates (clades) across a wide environmental gradient, which can limit statistical power for detecting the effects of environmental factors on SSRs. Second, sites can be small enough to have relatively homogeneous biotic and abiotic conditions, which makes characterizing the environments simpler and more reliable. Characterizing the large total area occupied by an entire clade is usually more complicated. Third, testing for causality through manipulative experiments should also be easier in site-based studies. Sites can be small enough for experiments to be feasible, whereas the geographical range of a clade is too large for experiments to be practical in most cases.

However, the limitation of the site-based approach is also concerned with spatial scale. Specifically, the larger the spatial scale we delineate sites at, the less extensively we can replicate them because of increasingly limited availability of sites. As a result, statistical power is more severely compromised in detecting effects that emerge only at larger scales. For example, allopatric speciation could be a major process by which sexual dimorphism affects the species diversity of a given site, as hypothesized by the differential fusion model [32], but allopatric speciation may often occur over large scales, particularly when the focal organisms have high dispersal ability (birds, flying insects, bird-dispersed plants, etc.). Consequently, site-based studies could overlook the role of speciation that might be detected by clade-based studies (Box 1). The site-based approach may work better for organisms with low dispersal ability (lake fishes, lizards, flightless insects and birds, dispersal-

Box 2. Experiments in Site-Based Studies

Neither a clade-based nor a site-based approach can definitively establish causality between sexual dimorphism and species diversity without experimental manipulation. Similarly, no environmental factor hypothesized to affect SSRs can be ascertained without experimental manipulation of that factor. An illustrative example of this problem comes from *Anolis* lizards on Caribbean islands. Schoener [1] suggested that the negative SSR found in these lizards might not indicate direct causality and that a third factor could explain the observed relationship. One such factor may be island accessibility. Due to dispersal limitation, remote islands may lack predators found on islands near the mainland from which predators immigrate [77,78]. When present, these predators can keep the island lizard population low, thereby weakening resource competition and leaving little pressure for the lizards to sexually diverge in resource-acquiring traits [23]. Meanwhile, nearby islands may also have more lizard species than remote islands because of the relative ease with which they themselves immigrate from the mainland. In this scenario, a negative SSR is expected, with more remote islands having greater sexual dimorphism and lower species diversity. However, dimorphism and diversity are both affected by a third factor, island accessibility, rather than having a direct causal relationship with each other.

Luckily, in site-based studies, experimental manipulation to rule out third factors should be possible provided the sites are small enough for site-scale manipulation. This feasibility is in contrast to clade-based studies, where experimental manipulation for the entire range of clades is in most cases impractical. For example, the site-based study by Pincheira-Donoso *et al*. [21] provided a compelling case for negative SSRs in the lizards they studied, but the presented evidence was correlational. The findings reported in this study could be assessed for causality through experimental manipulation of sexual dimorphism, species diversity, or both across replicated local sites. More generally, sexual dimorphism and species diversity can be manipulated in ways similar to how the sex ratio of newts in experimental ponds [72] and the presence of lizards on Caribbean islands [79] were manipulated in recent studies. These experiments would allow us to examine the invasibility of the communities, the types of species that can coexist, and the consequences for SSRs. Although hypotheses concerning speciation may be difficult to test experimentally, many organisms may often respond quickly enough for hypotheses concerning immigration, extinction, and niche differentiation to be experimentally testable [78,79].

limited plants, etc.), in which both sympatric and allopatric speciation can occur even within small, well-replicated sites.

Moving Forward

Given the differing sets of strengths and limitations of the two approaches, we suggest that the study of SSRs would benefit from wider applications of the site-based approach as well as combined applications of the site- and clade-based approaches. Site-based studies have the largely untapped potential to contribute to building more empirically informed hypotheses regarding the environmental conditions under which different hypotheses underlie SSRs. By comparing across sites that differ in the environmental factors of interest, it should be possible to infer which factor might influence SSRs, complementing insights from the clade-based approach. Furthermore, these inferences can be experimentally tested using sites as replicates for species introduction or removal (Box 2) in ways similar to how inferences from comparative phylogenetics can be tested experimentally [63]. In this case, however, comparisons and experiments would be performed across sites, not clades.

As an example, we can consider the hypothesis that sexual dimorphism either inhibits or promotes extinction (i.e., H3 or H4). One environmental factor that determines which hypothesis is true may be the sites' carrying capacity. For example, one prediction might be that in large populations, sexual selection inhibits extinction because sexual selection accelerates adaptation, whereas in small populations sexual selection promotes extinction because of an increased risk of demographic stochasticity [49]. Another possibility is that environmental factors that influence sex ratio affect whether sexual dimorphism inhibits or promotes extinction. For example, a population that has an even sex ratio may create a strongly competitive environment for both sexes, increasing the population's risk of extinction. By contrast, a population of the same species with the same extent of sexual dimorphism may have a weak competitive effect on individuals of the rare sex if the sex ratio is highly skewed, thus buffering the rare sex and consequently the population from extinction. Naturally, these site-based ideas can be more readily tested by site-based analyses than by clade-based ones (Box 2).

The form of SSRs is determined not solely by the local environmental characteristics of the sites, but also by dispersal and migration from the regional **species pool**, affecting the contribution of immigration to species diversity and sexual dimorphism (H5 and H9) [21]. Site-based analysis allows one to ask, for example, whether the variation among local sites in their distance to the regional species pool (e.g., distance from mainland to replicate islands), affecting the frequency of dispersal and migration, obscures or strengthens patterns of local SSRs that would be expected from the local hypotheses (H1–4 and H6–8). This question can be addressed by including the distance to the mainland (as a proxy for dispersal and/or migration frequency) in statistical models describing local SSRs (assuming the regional species pool is otherwise the same for different local sites). In addition, the contribution of immigration relative to *in situ* evolution can be addressed using null-model analyses like the one used by Poe *et al*. [64].

Because of the closely linked strengths and weaknesses of the clade- and site-based approaches, studies that directly combine the two approaches can be especially revealing. Specifically, we can use both sites and clades as replicates to ask whether sexual dimorphism and a certain environmental factor interact to affect species diversity. If a significant interaction effect were detected, that would indicate that the effect of sexual dimorphism on species diversity depends on the environmental factor, suggesting that the form of SSRs can be influenced by that factor. In addition to examining species diversity itself, we can also ask whether sexual dimorphism and the environmental factor interact to affect processes that alter species diversity and sexual dimorphism, including speciation, extinction, immigration, and niche differentiation, when appropriate data are available. These analyses can inform which of the hypotheses in Table 1 may be more likely to be operating. Inferences made through these analyses can then be tested experimentally, when feasible, to establish causality (Box 2).

As a specific example of this approach, we can take a look at Wagner *et al*. [17]. Using 166 cichlid lineages found in 46 African lakes, the researchers found a significant interaction effect of sexual dichromatism and lake depth on the extent of diversification. One possible explanation might be that sexual dichromatism more strongly facilitates speciation via pre-mating isolation in shallow lakes than in deep lakes because coloration is more visible in shallower lakes. Whatever the specific mechanism may be, a result like this would suggest that it is when lakes are shallow that one specific hypotheses (H1; i.e., the hypothesis that sexual dimorphism promotes speciation) is especially likely, resulting in a positive SSR. This strategy can be particularly powerful when site-based and clade-based approaches are combined because each site provides multiple data points whenever the site contains multiple clades, increasing the statistical power. Empirical systems to which the strategy we advocate here can be applied should not be limited to the African cichlids. For example, the Hawaiian picture-wing *Drosophila* and the Hawaiian damselfly *Megalagrion* may be good candidates for these analyses because multiple clades are found on several islands, including Kauai, Oahu, Maui Nui, and Hawaii [65,66].

Ultimately, diversification at large, macroevolutionary scales shapes the regional species pool from which species immigrate and subsequently undergo character displacement at local sites. In turn, species traits affected by local character displacement can influence the regional species pool [67–69]. To understand when this feedback between regional and local processes occurs and how the feedback affects SSRs, studies that apply both clade- and site-based approaches to the same system (e.g., [17]) should be particularly effective.

Concluding Remarks

We have argued for the utility of the site-based approach, but it should be clear by now that site-based studies do not replace clade-based studies. Rather, they are complementary. Establishing causality is challenging in any effort to explain large-scale phenomena, including SSRs. The joint use of the two approaches that combines evolutionary and community ecology should take us closer to answering why patterns of SSRs are so variable (see Outstanding Questions).

Outstanding Questions

What are the primary mechanisms underlying sexual dimorphism–species diversity relationships (SSRs)?

What are the environmental factors that determine the relative importance of the mechanisms shaping SSRs?

How does individual movement (dispersal and migration) affect the form of SSRs?

How and under what conditions do ecological interactions among distantly related clades affect the form of SSRs?

What phylogenetic scale is most suitable for analyses of SSRs? How can we determine the appropriate scale?

Does the form of SSRs differ depending on whether sexual dimorphism evolves via sexual selection, character displacement, or both?

How can clade-based analyses be best combined with site-based analyses to understand SSRs?

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