

Forum

Eco-Evolutionary
Dynamics of Sexual
Dimorphism

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Sexual dimorphism is widespread, but we have a limited understanding of its significance for communities and ecosystems. Several new experiments demonstrate that sexual dimorphism can have far-reaching ecological effects. These results suggest that sexual dimorphism and sexual selection are potent, but largely overlooked components of eco-evolutionary dynamics.

Eco-evolutionary dynamics describe reciprocal effects between evolution and population, community, and ecosystem ecology. These dynamics can be broadly important when natural selection causes rapid trait changes to occur in a population, because the trait changes can have community- and ecosystem-wide consequences [1] (Figure 1A). There may also be ecological consequences of evolutionary responses to sexual selection. This hypothesis is primarily supported by theory and experiments demonstrating that sexual selection can affect population ecology [2] and by work showing that sexual selection can affect functional traits (i.e., those hypothesized to have community or ecosystem effects) [3]. However, the role of sexual selection in communities and ecosystems remains largely untested.

Selection has community and ecosystem consequences through its effects on traits (Figure 1). Sexual selection can shape the trait distribution of a population by affecting

sexual dimorphism (i.e., the trait differences between females and males; arrow 2 in Figure 1B). Sexual dimorphism is ubiquitous in nature and encompasses a variety of traits that may impact community and ecosystem dynamics. Given the recent interest in understanding community and ecosystem effects of intraspecific trait variation in general [4], the lack of empirical research on the ecological consequences of sexual dimorphism is surprising (arrow 3, Figure 1B).

Evolved Sexual Dimorphism in Ecological Roles

There has long been evidence of ecological dimorphism (i.e., sexual dimorphism in ecological roles). For example, the sexes commonly differ in diets in the field. These effects may be pronounced in cases of sexual size dimorphism, in which the larger sex can feed on larger prey. In species without strong size dimorphism, ecological dimorphism may still be strong due to dimorphism in functional traits. For example, the sexes of the recently extinct huia (*Heteralocha acutirostris*), a New Zealand bird species that exhibited one of the most extreme cases of sexual dimorphism in beak shape known, must have fed on significantly different resources (Figure 2A) [5]. Another extreme ecological dimorphism is found in adult mosquitoes: females feed on animal blood, while males feed on plant nectar (e.g., *Ochlerotatus* sp., Figure 2B).

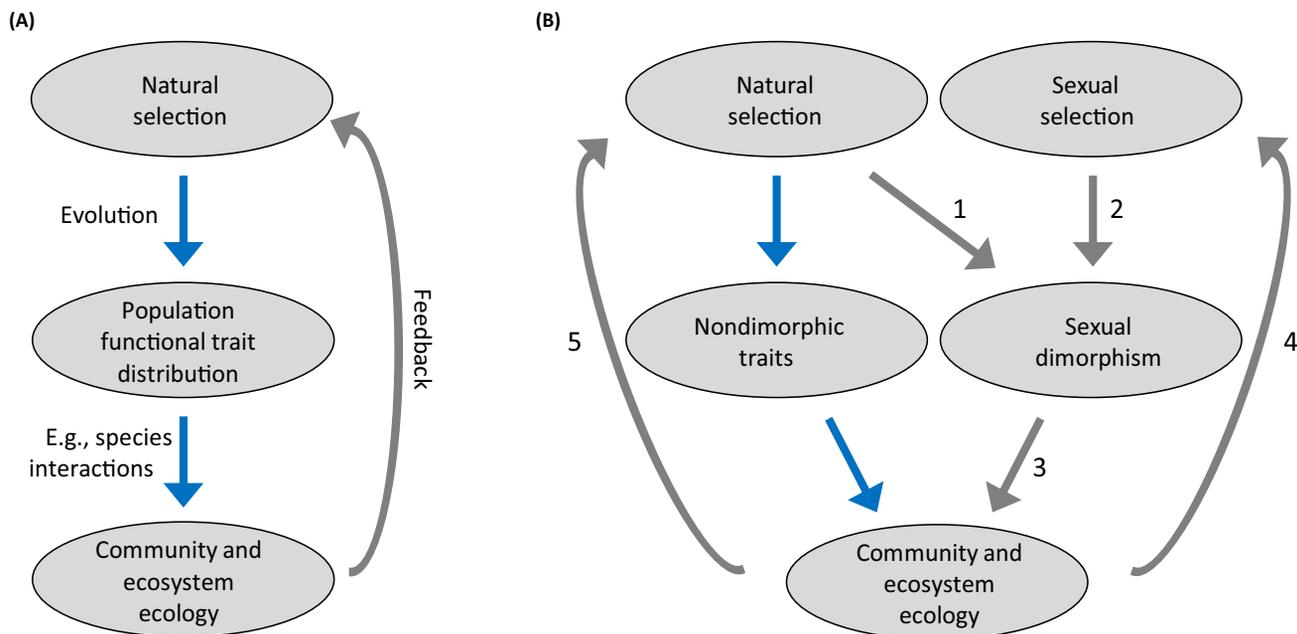
Ecological dimorphism could be significant even when sexual dimorphism is relatively inconspicuous. For example, the sexes may show little morphological dimorphism, but ecological dimorphism could arise from differential habitat use [6]. More generally, it may be that most sexual organisms display some degree of ecological dimorphism due to divergent nutritional requirements between the sexes, a product of differential reproductive investment. Even weak dimorphism could be important for communities and ecosystems in abundant or otherwise ecologically important populations.

Studies that correlate variation in ecological conditions to population or species variation in dimorphism are informative but cannot distinguish ecological causes from effects of dimorphism (e.g., [7]). Thus, experimental manipulations are needed to test for community and ecosystem effects of sexual dimorphism. Such direct tests have only recently emerged (arrow 3, Figure 1B) and have been performed at two levels of biological organization: the individual level and the population level.

The Extended Phenotype of Dimorphism

Sex differences at the individual level can have community and ecosystem consequences when communities assemble or ecosystems exist as 'extended phenotypes' of individual hosts (i.e., foundation species). For example, Nell and colleagues [8] demonstrated that female genotypes of the mulefat shrub (*Baccharis salicifolia*) had more flowers and grew more quickly than did male genotypes cultivated in the same garden (Figure 2C). This trait dimorphism led to dimorphism in hosted arthropod community composition; the more flower-laden females had higher predator densities, presumably because of increased visitation by nectar-feeding insect prey. Similarly, Tsuji and Fukami [9] studied the microbe communities assembling on male versus female flowers in the dioecious shrub *Eurya emarginata* (Figure 2D). Female flowers contained less nectar and had significantly lower bacterial and fungal concentrations compared with male flowers, apparently a result of differential visitation by insects. Based on this and related work, it may be that microbiomes are commonly forms of 'extended sexual dimorphism' in plants and animals.

Studying sexual dimorphism in the extended phenotypes of foundation species provides a clear-cut relationship between sexual dimorphism and community and



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Figure 1. The Conceptual Model. (A) The field of 'eco-evolutionary dynamics' has classically focused on the community and ecosystem effects of evolution by natural selection (blue arrows) and has not focused on sexually dimorphic traits. The field has further aimed to parse feedbacks between evolution and ecology when they act on similar timescales. (B) Recently, researchers have called for the explicit incorporation of sexual selection into this framework [2,3], which we expand in our conceptual model to include two separate aspects of the trait distribution of a population: sexually dimorphic traits and nondimorphic traits. While both natural selection (1) and sexual selection (2) affect sexual dimorphism (together, an effect referred to as 'sex-specific selection'), to understand the link between sexual selection and communities and ecosystems, we must understand the effect of sexual dimorphism on communities and ecosystems (3). Given that communities and ecosystems shape sexual selection (4) and natural selection (5), future work could aim to parse eco-evolutionary feedbacks associated with sexual dimorphism.

ecosystem ecology. However, there is often interest in communities and ecosystems assembling at larger spatial scales than those associated with individual hosts. Moreover, from the eco-evolutionary dynamics perspective, the overarching goal is to test the ecological effects of evolutionary change, which occurs in populations. Thus, the unifying level of analysis for understanding the effects of sexual dimorphism on communities and ecosystems, and incorporating those effects into an eco-evolutionary perspective, is at the population level.

Populations Link Dimorphism Evo to Eco

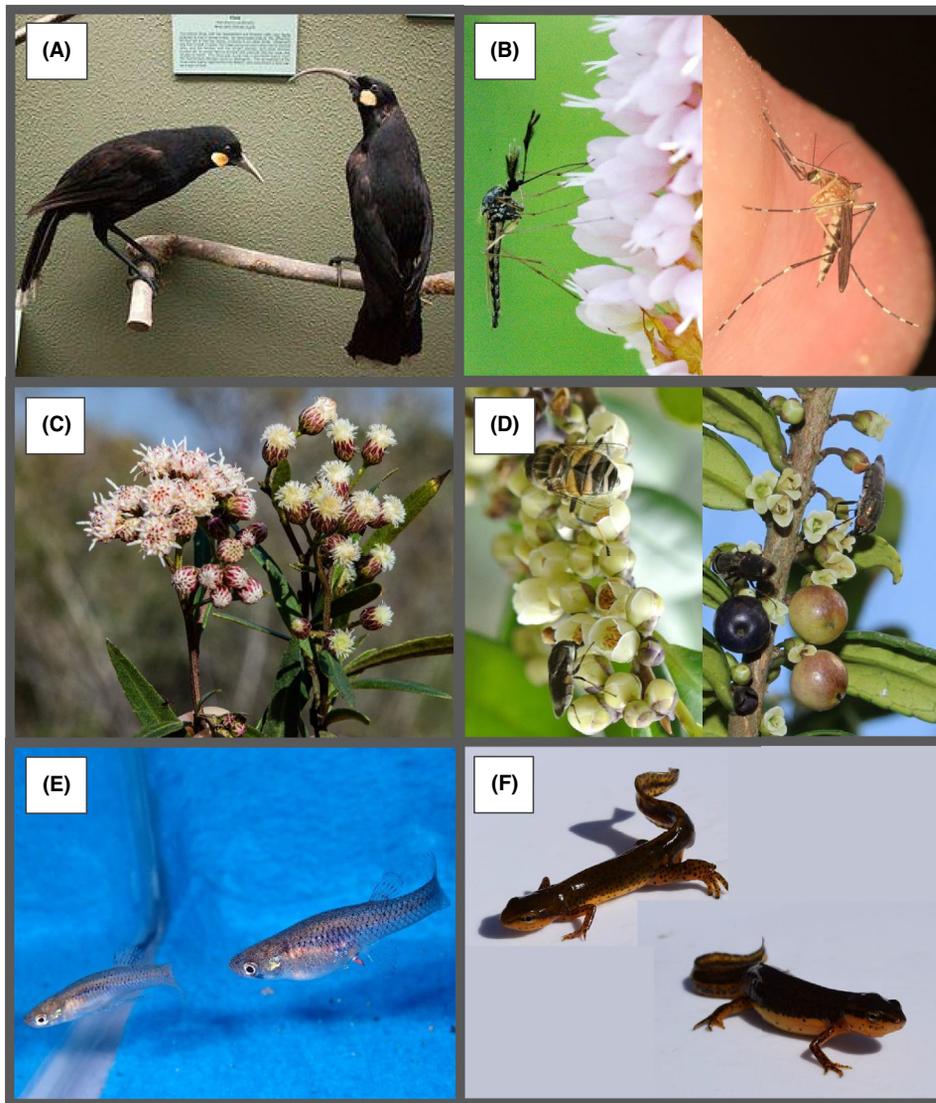
To date, effects of sexual dimorphism have been studied experimentally at the population level through the manipulation of population sex ratios. This approach

seeks to compare differences in effects of populations with trait distributions that are more female or male biased.

Fryxell and colleagues [10] manipulated population sex ratios of sexually dimorphic mosquitofish (*Gambusia affinis*) in pond mesocosms (Figure 2E). In contrast to male mosquitofish, females exhibit continuous growth and have higher feeding and excretion rates. In pond mesocosms, female-biased populations induced stronger trophic cascades, causing changes even to ecosystem properties such as water temperature and pH. When comparing the effect size of sex ratio (female-biased vs. male-biased) to the effect size of mosquitofish presence versus absence, sex ratio effects were up to approximately half as strong as the effects of mosquitofish presence itself. Thus, the strong and diverse

ecological effects of mosquitofish are largely shaped by the sex ratio of populations, which vary widely in nature.

In the other sex ratio experiment, Start and De Lisle [11] manipulated sex ratios of predaceous newts (*Notophthalmus viridescens*) in pond mesocosms (Figure 2F). While these newts do not show strong differences in feeding traits *per se*, the sexes differ substantially in habitat use. Results showed that female-biased populations spent more time in the benthic zone and grazed down benthic prey relative to pelagic prey, thus inducing a community shift towards the dominance of pelagic prey. These results highlight that, even in cases of inconspicuous morphological dimorphism, ecological effects of sexual dimorphism can still be significant.



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Figure 2. Taxa Described in the Main Text. Some of these taxa have hypothesized community and ecosystem effects of sexual dimorphism, (A) huia (*Heteralocha acutirostris*) and (B) mosquitoes (e.g., *Ochlerotatus* sp., pictured), whereas others from recent experiments show significant effects of sexual dimorphism, (C) mulefat (*Baccharis salicifolia*), a dioecious shrub from the American southwest; (D) a dioecious shrub from Japan (*Eurya emarginata*); (E) mosquitofish (*Gambusia affinis*); and (F) eastern North American newt (*Notophthalmus viridescens*). Some species show stark morphological dimorphism, while others show more cryptic dimorphism, for example, in traits such as nectar concentration (D) and habitat use (F). Females are pictured on the right, and males are pictured on the left in each instance. Photographs reproduced from K. Mooney (C), K. Tsuji (D), and D. Weiler (E).

Towards Sexual Dimorphism in an Eco-Evo Framework

Sex ratio manipulations are useful as approaches to understanding the effects of existing sexual dimorphism, but connecting results to ongoing evolution of

sexual dimorphism remains a challenge. In particular, sex ratio manipulations modify trait distributions in ways that are not evolved and, relatedly, they do not test how contemporary evolution of sexual dimorphism operates to influence eco-

evolutionary dynamics. Moreover, sex ratio manipulations confound dimorphism-shaped trait distributions with behaviors associated with ongoing sexual selection (e.g., male harassment of females increases with increasing male-

biased sex ratios). A hitherto unused approach that could overcome some of these issues would be to test how recently diverged populations with variable degrees or types of dimorphism might display divergent community and ecosystem effects while held at the same sex ratio.

Beyond such complications, the case studies we present reflect a narrow range of species and traits. We expect that other species and traits could display similarly important effects. For example, cryptic coloration in females may make them less vulnerable to predators, and the courting behaviors of males can involve clearing vegetation and moving substrate to create display arenas (a case of sex-specific ecosystem engineering). A greater diversity of tests will allow us to assess the generalities or idiosyncrasies of these effects.

Eco-evolutionary dynamics are characterized not only by evolutionary effects on ecological processes, but also by bidirectional feedbacks between ecology and evolution [1]. The full reciprocal feedback of how ecological effects of dimorphism in turn change selection and dimorphism is a frontier yet to be explored. Dimorphism-induced changes to ecology could either

affect the strength and pattern of sexual selection directly (arrow 4, Figure 1B) via its dependence on ecological context [12], or indirectly by affecting natural selection that acts together with sexual selection to shape dimorphism (arrow 1 via arrow 5, Figure 1B) [13]. Such feedback effects are challenging to test experimentally but could enrich our understanding of the links among natural selection, sexual selection, sexual dimorphism, and communities and ecosystems.

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